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# STUDIES IN THE THEORY OF DESCENT

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*WITH NOTES AND ADDITIONS BY THE AUTHOR*

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I.

LARVA AND IMAGO VARY IN STRUCTURE INDEPENDENTLY OF EACH OTHER.

It would be meaningless to assert that the two stages above mentioned were *completely* independent of one another. It is obvious that the amount of organic and living matter contained in the caterpillar determines the size of the butterfly, and that the quantity of organic matter in the egg must determine the size of the emergent larva. The assertion in the above heading refers only to the structure; but even for this it cannot be taken as signifying an absolute, but only a relative independence, which, however, certainly obtains in a very high degree. Although it is conceivable that every change of structure in the imago may entail a correlative change of structure in the larva, no such cases have as yet been proved; on the contrary, all facts indicate an almost complete independence of the two stages. It is quite different with cases of *indirect* dependence, such, for example, as are brought about by 'nurse-breeding.' This phenomenon is almost completely absent in Lepi-

doptera, but is found in Diptera, and especially in Hymenoptera in every degree. The larvæ of ichneumons which live in other insects, require (not always, but in most instances) that the female imago should possess a sharp ovipositor, so that in this case also the structure and mode of life of the larva influences the perfect insect. This does not depend, however, on inherent laws of growth (correlation), but on the action of external influences, to which the organism endeavours to adapt itself by natural selection.

I will now let the facts speak for themselves.

It is shown by those species in which only one stage is di- or polymorphic that not every change in the one stage entails a corresponding change in the other. Thus, in all seasonally dimorphic species we find that the caterpillars of butterflies which are often widely different in the colour and marking of their successive generations are absolutely identical. On the other hand, many species can be adduced of which the larvæ are dimorphic whilst the imagines occur only in one form (compare the first and second essays in this volume).

There are however facts which directly prove that any one stage can change independently of the others ; I refer to the circumstance that any one stage may become independently variable—that the property of greater variability or of greater constancy by no means always occurs in an

equal degree in all the three stages of larva, pupa, and imago, but that sometimes the caterpillar is very variable and the pupa and imago quite constant. On the other hand, all three stages may be equally variable or equally constant, although this seldom occurs.

If variability is to be understood as indicating the period of re-modelling of a living form, whether in its totality or only in single characters or groups of characters, from the simple fact of the heterochronic variability of the ontogenetic stages, it follows that the latter can be modified individually, and that the re-modelling of one stage by no means necessarily entails that of the others. It cannot however be doubted that variability, from whatever cause it may have arisen, is in all cases competent to produce a new form. From the continued crossing of variable individuals alone, an equalization of differences must at length take place, and with this a new, although not always a widely deviating, constant form must arise.

That the different stages of development of a species may actually be partly variable and partly constant, and that the variable or constant character of one stage has no influence on the other stages, is shown by the following cases, which are, at the same time, well adapted to throw light on the causes of variability, and are thus calculated to contribute towards the solution of the main problem with which this investigation is concerned.



When, in the following pages, I speak of *variability*, I do not refer to the occurrence of local varieties, or to variations which occur in the course of time, but I mean a high degree of individual variability—a considerable fluctuation of characters in the individuals of one and the same district or of the same brood. I consider a species to be constant, on the other hand, when the individuals from a small or large district differ from one another only to a very slight extent. Constant forms are likewise generally, but not invariably, such as are poor in local varieties, whilst variable forms are those which are rich in such variations. Since the terms “variable” and “constant” are but relative, I will confine myself to the most extreme cases, those in which the individual peculiarities fluctuate within very wide or very narrow limits.

As no observations upon the degree of variability shown by a species in the different stages of its development were available, I was obliged to fall back upon my own, at least so far as relates to the larval and pupal stages, whilst for the imaginal stage the wide experience of my esteemed friend Dr. Staudinger has been of essential service to me.

Let us in the first place confine our attention to the three chief forms which every Lepidopteron presents, viz. larva, pupa, and imago. With respect to the constancy or variability of these three forms, we actually find in nature all the

combinations which are theoretically conceivable.

(1.) There are species which possess a high degree of constancy in all three stages, such, for example, as *Limenitis Camilla*, *Pieris Brassicæ*,<sup>1</sup> *Sphinx Ligustri*, and *Euchelia Jacobææ*.

(2.) There are species showing a high degree of variability in all three stages. This case must be of rare occurrence, as I am only able to adduce *Araschnia Prorsa-Levana*, a fact which arises from the circumstance that the pupal stage is, as a rule, but seldom variable.

(3.) There are species which are variable in two stages and constant in the third. To this class, for example, belongs *Smerinthus Tiliæ*, of which the larva and imago are very variable, whilst the pupa is quite constant. The same is the case with *Lasiocampa Pini*, the well-known fir moth. Many butterflies show this same phenomenon in other combinations, such, for instance, as *Vanessa Urticæ* and *Polychloros*, in which the larva and pupa are very variable, and the imago very constant. In a less degree the same is also the case with *Vanessa Atalanta*, whilst in *Pieris Napi* the

<sup>1</sup> [The slight variability in the colour of this pupa, opens up the interesting question of the photographic sensitiveness of this and other species, which is stated to cause them to assimilate in colour to the surface on which the larva undergoes its final ecdysis. Some experiments upon this subject have been recorded by Mr. T. W. Wood, Proc. Ent. Soc. 1867, p. xcix, but the field is still almost unexplored. R.M.]

pupa and imago are variable, and the caterpillar remarkably constant, this likewise being the case with the local form *Bryonia*, which, according to my theory, is to be regarded as the parent form of *Napi* (See Part I. of the present volume).

(4.) There are species which are constant in two stages, and variable only in the third. Thus, a few species can be found in which the larva and pupa are constant and the imago variable. This is the case with *Saturnia Yamamai*, the imago of which is well known to present numberless shades of colour, varying from light yellow to greyish black, whilst the green caterpillar shows only slight individual differences of marking, and scarcely any differences of colour. The pupa of this species is quite constant. *Arctia Caja* and *Hebe*, and *Chelonia Plantaginis* belong to this same category.

There are a very large number of species which possess very constant imagines and pupæ, but extremely variable larvæ. The following are the cases known to me:—*Macroglossa Stellatarum*, *Fuciformis* and *Bombyliiformis*; *Chærocampa Elpenor*, *Celerio*, and *Nerii*; *Deilephila Galii*, *Livornica*, Hübn., *Hippophaës*, *Vespertilio*, and *Zygophylli*; *Sphinx Convolvuli*; *Acherontia Atropos*; *Smerinthus Ocellatus* and *Tiliæ*; *Callimorpha Hera*; *Cuculiia Verbasci* and *Scrophulariæ*.

Cases in which the variability depends entirely upon the pupa, while the larva and imago are



extremely constant, are of great rarity. *Vanessa Io* is a case in point, the pupa being light or dark brown, or bright golden green, whilst in the two other stages scarcely any light shades of colour or variations in the very complicated marking are to be met with.

The facts thus justify the above view that the individual stages of development change independently—that a change occurring in one stage is without influence on the preceding and succeeding stages. Were this not the case no one stage could possibly become variable without all the other stages becoming so. Did there exist a correlation between larvæ, pupæ, and imagines of such a nature that every change in the larva entailed a corresponding change in the imago, as soon as a large number of larval characters became fluctuating (*i.e.* as soon as this stage became variable), a large number of imaginal characters would necessarily also become fluctuating (*i.e.* this stage would also become correspondingly variable).

There is one other interpretation which might perhaps be attempted from the point of view of the old doctrine of species. It might be said that it is a special property of certain larval or imaginal markings to be variable whilst others are constant, and since the larval and imaginal markings of a species are generally quite distinct, it may easily happen that a butterfly possessing markings having

the property of constancy may belong to a caterpillar having variable markings.

There is a soul of truth underlying this objection, since it is true that the various forms of markings which occur in Lepidoptera apparently reach different degrees of constancy. If we speak of the constancy or variability of a species, a different meaning is attached to these expressions according as we are dealing *e.g.* with a species of *Sphinx* or a species of *Arctia*. That which in the latter would be estimated as a high degree of constancy, in the former would be taken as a considerable amount of variability. It is of interest, in connection with the question as to the causes of constancy, to note that the power of any form of marking to attain to a high degree of constancy is by no means inversely proportional to the complication of the marking, as would have been expected *à priori*.

Thus, the species of *Sphinx* and of allied genera possess on their fore-wings, which are mostly coloured with a mixture of dull grey, white and black, an exceedingly complicated arrangement of lines which, in constant species, show a high degree of uniformity : on the other hand, the chequered fore-wings of our *Arctiideæ*, which are far more coarsely marked, always show, even in the most constant species, well-marked individual differences. The different types of marking must therefore be measured by different standards.

But in granting this, we decidedly refute the statement that constancy and variability are inherent properties of certain forms of marking.

This reasoning is based on the simple fact that a given type of marking comprises both species of great constancy and of (relatively) great variability.

Thus, the fore-wings of *Sphinx Ligustri* and *S. Convolvuli* are extremely constant, whilst the very similarly marked *Anceryx (Hyloicus) Pinastri* is exceedingly variable. Similarly *Deilephila Euphorbiæ* is known by its great variability of colouring and marking, whilst *D. Galii*, which resembles this species so closely as to be sometimes confounded with it, possesses a high degree of constancy, and further, the Corsican and Sardinian *D. Dahlii* is very variable. Among the family *Arctiidae*, *Callimorpha Hera* and the Alpine *Arctia Flavia* are cases of constancy, whilst *A. Caja*, which is so similar to the last species, is so generally variable that two perfectly identical specimens can scarcely be found together.

The same can be shown to hold good for the markings of caterpillars. Thus, the larva of *D. Dahlii* shows very considerable variability, whilst that of *D. Galii* is very constant in marking (disregarding the ground-colour). So also the larva of *Vanessa Urticæ* is very variable and that of *V. Antiopa* very constant, &c.

The great differences with respect to constancy or variability which are displayed by the different

stages of one and the same species, must therefore find their explanation elsewhere than in the type of the marking itself. The explanation must be found in the circumstance that each stage changes independently of the others, and at different periods can enter a new phase of variability.

Q We are here led in anticipation to the main question :—Are changes produced by internal or external causes ? is it the physical nature of the organism which is compelled to become remoulded spontaneously after the lapse of a certain period of time ? or does such modification only occur when produced directly or indirectly by the external conditions of life ?

X In the cases before us the facts undoubtedly indicate a complete dependence of the transformations upon external conditions of life.

The independent appearance of variability in the separate stages of the metamorphosis might, however, be regarded as only apparent. It might still be attempted to attribute the changes to a purely inherent cause, *i.e.*, to a phyletic vital force, by assuming that the latter acts periodically in such a manner that at first one and then the following stage becomes variable, until finally the entire species is transformed.

There is but little to be said in reply to this if we once take refuge in entirely unknown forces, the operation of which can be arbitrarily conceived to be either constant or periodic.

But granting that such a transforming power



exists and acts periodically, the variability must always pass over the different stages in a fixed direction, like a wave over the surface of water—imago, pupa, and larva, or larva, pupa, and imago, must *successively* become variable. Cases like that of *Araschnia Prorsa*, in which all three stages are variable, may certainly be thus explained, but those instances in which the larva and imago are extremely variable, and the pupa quite constant, are entirely inexplicable from this point of view.

The latter can, however, be very simply explained if we suppose the changes to be dependent upon external influences. From this standpoint we not only see how it is possible that an intermediate stage should remain uninfluenced by the changes which affect the two other stages, but we can also understand why it should just be the pupal stage that plays this part so frequently. If we ask why most pupæ are constant and are relatively but very slightly variable, the answer will be found in the facts that all pupæ which remain concealed in the earth or inside plants (*Sesiidæ*), or which are protected by stout cocoons, show complete constancy, whilst any considerable amount of variability occurs only in those pupæ which are suspended or openly exposed. This is closely connected with a fact to which I have called attention on a former occasion,<sup>2</sup> viz., that

<sup>2</sup> "Über den Einfluss der Isolirung auf die Artbildung."  
Leipzig, 1872, p. 20.

dimorphism occurs in certain pupæ, but only in those which are openly exposed and which are therefore visible to their foes. I am only acquainted with such cases among the pupæ of butterflies, and it is likewise only among these that I have found any considerable amount of variability.

Facts of this kind indicate that Nature does not uselessly sport with forms, but that at any rate changes of this sort result from external influences. The greater frequency of variability among larvæ and its comparative rarity in imagines is also undoubtedly in favour of this view.

It has already been shown that species with variable larvæ and constant imagines are extremely common, but that those with constant larvæ and variable imagines are very rare. This confirms the conclusions, already drawn above, first, that the variability of the imago cannot owe its existence to the variability of the larvæ, and secondly, that the causes which produce variability affect the larval condition more commonly than that of the imago.

Where can these causes be otherwise sought than in the external conditions of life, which are so widely different in the two stages, and which are much more variable for the larva than for the imago?

Let us take the species of one genus, *e.g.* those of *Deilephila*. The imagines of our European

species—as far as we know—all live in precisely the same manner; they all fly at twilight,<sup>3</sup> showing a preference for the same flowers and very often frequenting the same spots, so that in the haunts of one species the others are almost always to be met with, supposing them to occur in the same locality. They conceal themselves by day in similar places, and are attacked by similar foes.

It is quite different with the caterpillars. These, even in the case of the most closely allied species, live under different conditions, as appears from the fact that they feed on different plants. The latter can, however, produce changes both directly and indirectly. The larvæ may acquire adaptive colours and markings, and these would vary in accordance with the colour and structure of the food-plant; or they may become brightly coloured as a sign of distastefulness in cases where they are inedible. Then again the colour of the soil on which the larvæ live would act upon their colours making these adaptive. Certain habits of the caterpillars may also be dependent upon the nature of their food-plants. Thus, *e. g.* *Deilephila Hippophaës* feeds only at night, and conceals itself by day under moss and among the leaves at the base of the food-plant; but *D. Euphorbia* could not acquire such a habit, because *Euphorbia*

<sup>3</sup> In some instances *Deilephila Lineata* has also been seen by day hovering over flowers.

*Cyparissias* generally grows on arid soil which is poor in vegetation, and which therefore affords no concealment, and furthermore, because a caterpillar, as long as it continues to feed, cannot, and as a matter of fact does not, ever wander far from its food-plant. A habit of concealment by burying in the earth also, such for example as occurs in *Acherontia Atropos*, could not be acquired by *D. Euphorbiæ*, because its food-plant generally grows on hard, dry, and stony ground.

In addition to these considerations, the foes would be different according as the caterpillar lived on plants which formed dense thickets covering large extents of the shore (*Hippophae*), or grew isolated on dry hillocks and declivities where the herbage was scanty or altogether absent; or again, according as the insect, in conjunction with such local differences, fed by day or had acquired the habit of feeding only by night. It must in fact be admitted that new and improved adaptations, or, in more general terms, that inducements to change, when depending on the environment, must be more frequently dissimilar for larvæ than for the imagines. We must accordingly expect to find actual change, or that condition of variability which may be regarded as initiative to change, occurring more commonly in larvæ than in perfect insects.

Since facts are in complete accordance with the results of these *à priori* considerations we may also venture to conclude that the basis of the consider-



ations is likewise correct, viz., the supposition that the changes of colour and marking in caterpillars, pupæ, and imagines result from external influences only.

This must not be taken as signifying that the single stages of the larval development are also only able to change through the action of external influences. The larval stages are correlated with each other, as has already been shown (see the previous essay): new characters arise in the adult caterpillar at the last stage and are then gradually transferred back to the younger stages quite independently of external influences, this recession being entirely brought about by the laws of correlation. Natural selection here only exerts a secondary action, since it can accelerate or retard this transference, according as the new characters are advantageous or disadvantageous to the younger stages.

Now as considerable individual differences appear in the first acquisition of a new character with respect to the rapidity and completeness with which the individuals acquire such a character, the same must obtain for the transference of an improvement acquired in the last stage to the next younger stage. The new character would be acquired by different individuals in different degrees and at different rates—it would have, to a certain extent, to struggle with the older characters of the stage; in brief, the younger stage would become variable.

Variability of this kind might well be designated as *secondary*, in contradistinction to *primary* variability; the latter (primary) depends upon an unequal reaction of the individual organisms to external influences, the former (secondary) results from the unequal strength and rate of the action of the innate laws of growth governing the organism. In both cases alike exceeding variability may occur, but the causes producing this variability are dissimilar.

The different stages of larval development would thus frequently display independent variability in a manner similar to the pupal or imaginal stages, since they can show individual variability while the other stages of development remain constant. This appearance of independent variability in the different stages of the larval development, however, is in truth deceptive—we have here in fact a kind of wave of variability, which passes downwards through the developmental stages, becoming gradually weaker, and finally dying out completely.

In accordance with this, we very frequently find that only the last or two last stages are variable, while the younger stages are constant. Thus in *Macroglossa Stellatarum*, the larvæ are constant in the first, second, and third stages, but become variable in the fourth, and in the fifth stage first show that high degree of variability which has already been described in detail (See. Pl. III., Figs. 3—12).

The larva of *Vanessa Cardui* also, according to my notes, are extremely constant in the first four stages in spite of their complicated marking, but become variable in the fifth stage, although to no very great extent.

In *Smerinthus Tiliæ*, *Ocellatus* and *Populi* also, the greatest larval variability is shown only in the last stage, the preceding stages being very constant. These cases by no means depend upon the marking of the young stages being simpler and therefore being less capable of varying. The reverse case also occurs. In a somewhat similar manner as the young of the tapir and wild hog are striped, while the adult animals are plainly coloured, the young caterpillars of *Saturnia Yamamai* possess longitudinal black lines on a yellow ground, while as early as in the second stage a simple green colour appears in the place of this complicated but perfectly constant marking. If the young stages are so frequently constant, this rather depends upon the fact that the transference of a new character to these stages not only takes place gradually, but also with continually diminishing energy, in a manner somewhat similar to physical motion, which continually diminishes in speed by the action of resistance till it is completely arrested. This constancy of the younger stages may further be due to the circumstance that the characters would only be transferred when they had become fixed in the last stage, and were

consequently no longer variable. The transferred characters may thus have acquired a greater regularity, *i. e.* a less degree of variability, than they possessed at their first origination. Extensive investigations in this special direction must be made if the precise laws, in accordance with which the backward transference of new characters takes place, are to be discovered. By such researches only should we arrive with certainty at the causes which determine the lesser variability of the young larval stages.

It may also occur that the early stages are variable, whilst the later stages are constant, although this case appears to happen less frequently. Thus, the caterpillars of *Gastropacha Quercifolia* vary considerably in the second stage but are constant at a later period, and the same is the case with *Spilosoma Urticæ*, which in the second stage may be almost considered to be dimorphic, but which subsequently becomes constant.

Cases in which the first stage is variable appear to be of the least frequent occurrence. I know of only one such instance, viz., *Anceryx Pinastri*, of which the newly-hatched larvæ (Pl. VI., Fig. 53) show considerable differences in the brownish-black crescentic spots. The second (Fig. 54), third, and fourth stages are then tolerably constant, while the fifth stage again is very variable.

An instance of this kind can be easily explained by two waves of variation, the first of which now



affects only the first stage, while the second has just commenced to affect the fifth stage. Such a supposition is not opposed to any theoretical considerations, but rather has much probability in its favour, since we know that species are from time to time subject to be remodelled; and further, that the coalescence of several stages of phyletic development in the ontogeny of one and the same species (see p. 226, development of the genus *Deilephila*) shows that during the backward transference of one character, new characters may appear in the last stage of the ontogeny, and indeed very frequently at a time when the next youngest character has not been transferred back so far as to the first stage.

That this secondary variability is to a certain extent brought about by the conflict between the old and new characters, the latter striving to suppress the former, is shown by the caterpillar of *Saturnia Carpini* which I have observed for many years from this point of view, and than which I do not know a more beautiful illustration.

When these larvæ leave the egg they are black, but in the adult state are almost bright green—this at least being the case in a local form which, from the district in the vicinity of Genoa where it is found, I will designate as the var. *Ligurica*. Now whilst these two extreme stages of development are relatively constant, the intermediate stages show a variability which becomes

greater the nearer the last stage is approached, this variation in the marking depending simply on the struggle between the green colour and the more anciently inherited black. In this manner there arises, especially in the fourth stage of the German local form, an incredible mixture of the most diverse markings, all of which can, however, be very easily explained from the foregoing point of view.

The simpler and, as I am inclined to believe, the older form of the transformation is presented to us in the local variety *Ligurica*. In the last stage, when 7.5 centimeters long, this form is of a beautiful bright green colour without any trace of black marking<sup>4</sup> (Pl. VIII., Fig. 77). The colour of the six orange warts which are situated on each segment is also similar in all specimens, so that this stage is perfectly constant.

Our German *S. Carpini* shows different characters in the fifth stage. It is true that individual specimens occur which are entirely green without any black, but these are rare; the majority possess a more or less broad black ring encircling the middle of each segment (Pl. VIII., Figs. 78 and 79). Those specimens in which the black ring has become broken up into large or small spots

<sup>4</sup> It is true that I only reared one brood, but from this fifty specimens were obtained. It would be interesting to know whether this variety of the caterpillar is distributed over the whole of Southern Europe.

surrounding the base of the warts constitute intermediate forms (Fig. 80). The last stage of the German local form, unlike that of the Genoese local form, is therefore very variable.

The two forms, moreover, do not simply differ in being more or less advanced in phyletic development, but also in several other points. As it is of great theoretical interest to show that a species can develop local differences only in the stage of larva, I will here subjoin the plain facts.

The differences consist in that the Genoese local form goes through five moults whilst the German local form, like most caterpillars, has only four moults. Further, in the Genoese form the light green, which is also possessed by the German form in the fourth stage, when it once appears, is retained to the end of the larval development, whilst in the fifth stage of the German form this colour is replaced by a dull greyish-green (compare Figs. 77 and 78). There is further a very considerable difference in the earlier stages which shows that the phyletic transforming process has taken a quite independent course in the two forms. Since the struggle between the green and black—retaining this idea—appears to be quite finished in the last stage of the Genoese form, we should expect that the new colour, green, would now also have encroached further upon the younger stages than in the German form. Nevertheless, this is not the case, but quite the reverse happens, the

black maintaining its ground longer in the Italian than in the German form.

In the Genoese form the two first stages are completely black, and in the third stage an orange-yellow lateral stripe first appears. In the German form this stripe appears in the second stage, and there is not subsequently added, at least on the middle segments, a yellow border surrounding some of the warts of the median series. In the third stage, however, the yellow (which is but the precursor of the later green colour) becomes further extended, so that the caterpillars often appear of an orange colour, some or all of the warts and certain spots and stripes only being black (Figs. 66 and 68). The warts are also often yellow while the ground remains in most part black—in brief, the bright colour is in full struggle with the black, and an endless series of variations is the result of this conflict, whilst in the corresponding stage of the Genoese form almost complete constancy prevails.

This constancy remains also in the following (fourth) stage, the caterpillar still being deep black, only the yellow (sulphur-coloured) lateral stripe, which has now become brighter, indicating the impending change (Fig. 67). This takes place in the fifth stage, in which the ground-colour suddenly becomes bright green, the black remaining at most only in traces on the anterior edges of the segments.



This is the same marking as is shown by the fourth stage of the German form, only in this case individuals quite destitute of black do not occur. In many specimens indeed black forms the ground colour, the green only appearing in certain spots (Figs. 71 to 75); in others the green predominates, and these two extremes are connected by innumerable intermediate forms, so that this stage must be regarded as the most variable of all.

The sixth stage of the Genoese and the fifth of the German form have already been compared together. The results may be thus tabulated :—

<i>A. German form.</i>	<i>B. Genoese form.</i>
STAGE I. 9 days. Black ; constant.	9 days. Black ; constant.
STAGE II. 8 days. Black, with orange-yellow lateral stripe ; variable.	11 days. Black ; constant.
STAGE III. 5 days (in some cases as much as 16 days). Black, with yellow ; very variable.	12 days. Black, with orange-yellow lateral stripes ; constant.
STAGE IV. 16 days (in some cases only 5 days). Bright green and black, mixed ; very variable.	6 days. Black, with bright yellowish lateral stripe ; constant.
STAGE V. 6 days (frequently longer). Dark green, with or without black bands ; variable.	6 days. Bright green, small traces of black ; variable.
STAGE VI. Pupation.	18 days. Bright green, without any black ; constant.
	STAGE VII. Pupation.

From this comparison we perceive that the process of transformation has at least become preliminarily concluded in the Genoese form. Why the backward transference of the newly-acquired character to the young stages has not yet occurred, or, at least, why it is not in progress, does not appear; neither can it be stated whether this will take place later, although we may venture to suppose that such will be the case. At first sight but a relatively short time appears necessary for the single stage V., which is still in a state of fluctuation (variable), to become constant by continued crossing, like all the other stages.

That the transformation is still in full progress in the German form, is shown by the fact that in this case all the stages are variable with the exception of the first—the second stage being only variable to a small extent, the third to a much greater extent, and the fourth to the highest degree conceivable, whilst the fifth and last stage is again less variable—so that the greatest struggle between the old and new characters takes place in the fourth stage.

Among the innumerable variations presented by this last stage a complete series of transitional forms can be arranged so as to show the gradual conquest of the black by the green, and thus indicating, step by step, the course which the latter colour has taken.

In the blackest specimens there is nothing

green but the lateral (infra-spiracular) line which was yellow in the preceding stage, and a crescent-shaped streak at the base of the middle warts together with a still smaller crescent at the base of the upper warts (Figs. 71 and 81). These spots become extended in lighter specimens and approximate so as to leave only narrow black bridges, a third spot being added at the posterior edge of the warts (Figs. 72 and 82). The three spots then extend on all sides, still leaving for a long period narrow black lines at the boundaries where their growth has caused them to abut. In this manner there frequently arises on the green ground a true hieroglyphic-like marking (Figs. 85 and 86). Finally the black disappears from the anterior edge and diminishes on the middle line of the back where it still partly remains as a T-shaped figure (Figs. 73 and 74), although generally replaced elsewhere by the green with the exception of small residues.

One point remained for a long time inexplicable to me, viz., the change of the light green into dark grey-green which appeared in the last stage in connection with a total change of the black marking.

Supposing that new characters are actually acquired only in the last stage, and that from this they are transferred to the younger stages, we should expect to find completely developed in the last stage the same colouring and markings as

are possessed more or less incompletely in the fourth stage. Now since the developmental tendency to the removal of black and to the predominance of green—if we may thus venture to express it—is obvious in the fourth stage, we may expect to find in the fifth stage a bright green ground-colour, either without any mixture of black or with such black spots and streaks as were retained in the fourth stage as residues of the original ground-colour. But instead of this the fifth stage shows a dark green colour, and a more or less developed black marking which cannot in any way be derived from that of the fourth stage.

The Genoese local form observed last year first gave me an explanation to the extent that in this form the last stage is actually only the potential penultimate stage, or, more correctly expressed, that the same characters which at present distinguish the last stage of this form, are already more or less completely transferred to the penultimate stage.

The apparently paradoxical behaviour of the German form can be explained by supposing that before the pure bright green had become completely transferred to the penultimate stage a further change appeared in the last stage, the green ground-colour becoming darker, and black transverse bands being formed. The marking of the last stage would then be regarded as the reverse of that of the preceding stage; the absence



of black would be the older, simple black spots at the base of the warts the next in succession, and a connected black transverse band the most advanced state of the development.

Whether this explanation is correct, and if so, what causes have produced the second change, may perhaps be learnt at some future time by a comparison with the ontogeny of other *Saturniidae*; in the meantime this explanation receives support from another side by the behaviour of the Genoese local form. If the last stage of the German form has actually commenced to be again re-modelled, then this variety is further advanced in phyletic development than the Genoese form; and this corresponds entirely with the theory that in the former the light colour (the orange considered as preliminary to the transformation into green) has already been carried down into the second stage, whilst in the Genoese variety even in the fourth stage only the first rudiments of the colour-transformation show themselves.

The Genoese form is to a certain extent intermediate between the German form of *Saturnia Carpini* and the nearly related *S. Spini*, a species inhabiting East Germany. In this latter the larvæ, even in the adult state, are completely black with yellow warts. This form of caterpillar must therefore be regarded as phyletically the oldest, and this very well agrees with the character of the moth, which differs essentially from *S.*

*Carpini* only in not being sexually dimorphic. In *Carpini* the male possesses a far more brilliant colouring than the female, the latter agreeing so completely with the female of *Spini* that it can hardly be distinguished therefrom, especially in the case of the somewhat larger South European specimens of the last species. Now as the more simple colouring of the female must in any case be regarded as the original form, we must consider *Spini*, both sexes of which possess this colouring, to be phyletically the older form, and *Carpini*, the male of which has become differently coloured, must be considered as the younger type. This completely accords with the characters of the larvæ.

I must here mention that I have also asked myself the question whether the variations of the different larval stages are connected together as cause and effect—whether the lightest specimens of the fifth stage may perhaps not also have been the lightest individuals of the third and fourth stages.

Such relationship is only apparent between the third and fourth stages; the darkest larvæ of the third stage become the darker varieties of the fourth stage, although it is true that the lighter forms of the third sometimes also become dark varieties in the fourth stage. Between the fourth and fifth stages there is scarcely any connection of this kind to be recognized. Thus, the darkest

varieties of the fourth stage sometimes become the lightest forms of the fifth stage, whilst in other cases from the lightest individuals of the fourth stage there arise all the possible modifications of the fifth stage. Further details may be omitted: the negative result cannot cause any surprise, as it is a necessary consequence of the continued crossing that must take place.

We thus see that the three chief stages of development (larva, pupa, and imago) actually change in colour independently of each other, the single stages of the larval development being however in greater dependence upon one another, and being connected indeed in such a manner that a new character cannot be added to the last stage without being transferred in the course of time to the preceding stage, and at a later period from this again even to the youngest stage, supposing it not to be previously delayed in the course of its transference by unknown opposing forces. On this last point, however, the facts at present available do not admit of any certain decision.

But why do the individual larval stages behave in this respect so very differently to the chief stages of the whole development? why are the former so exactly correlated whilst the latter are not? If new characters have a general tendency to become transferred to the younger ontogenetic stages, why are not new imaginal characters first transferred to the pupa, and finally to the larva?

The answer to these questions is not far to find. The wider two stages of a species differ in structure, the less does correlation become possible; the nearer the two stages are morphologically related, the more powerful does the action of correlation become. It is readily conceivable that the more widely two succeeding stages deviate in structure and mode of life, the less possible does it become for characters to be transferred from one to the other. How is it possible, for example, that a new character in the proboscis or on the wings of a butterfly can be transferred to the caterpillar? If such correlation existed it could only manifest itself by some other part of the caterpillar changing in correspondence with the change of the proboscis or wings of the butterfly. That this is not the case has, in my opinion, been conclusively shown by all the foregoing considerations respecting the independent variability of the chief stages of the metamorphosis.

There are, moreover, an endless number of facts which prove the independence of the individual stages of development—I refer to the multitudinous phenomena presented by metamorphosis itself. The existence of that form of development which we designate as metamorphosis is alone sufficient to prove incontestibly that the single stages are able to change independently of one another to a most remarkable extent.

If we now ask the question: how has the so-



called "complete" metamorphosis of insects arisen? the answer can only be: through the gradual adaptation of the different stages of development to conditions of life which have continually deviated more and more widely from each other.<sup>5</sup>

But if individual stages of the post-embryonic development can finally attain to such complete diversity of structure as that of the larva and imago through gradual adaptations to continually diverging conditions of life, this shows that the characters acquired by the single stages are always only transferred to the same stages of the following generation, whilst the other stages remain uninfluenced thereby. This depends upon that form of heredity designated by Darwin "inheritance at corresponding periods of life," and by Haeckel "homochronic heredity."

<sup>5</sup> In this sense Lubbock says:—"It is evident that creatures which, like the majority of insects, live during the successive periods of their existence in very different circumstances, may undergo considerable changes in their larval organization in consequence of forces acting on them while in that condition; not, indeed, without affecting, *but certainly without affecting to any corresponding extent*, their ultimate form."—"Origin and Metamorphoses of Insects," London, 1874, p. 39.

## II.

DOES THE FORM-RELATIONSHIP OF THE LARVA  
COINCIDE WITH THAT OF THE IMAGO?

HAVING thus established the independence in the variability of the individual stages of metamorphosis, I will now turn to the consideration of the question as to how far a parallelism is displayed in the phyletic development of these stages. Is there a complete congruence of form-relationship between larvæ on the one hand and imagines on the other? does the classification founded on the morphology of the imagines agree with that based on the morphology of the larvæ or not?

If, according to Claus,<sup>1</sup> we divide the order Lepidoptera into six great groups of families, it is at once seen that these groups, which were originally founded exclusively on imaginal characters, cannot by any means be so clearly and sharply defined by the larval characters.

This is certainly the case with the *Geometræ*, of which the larvæ possess only ten legs, and on

<sup>1</sup> "Grundzüge der Zoologie," 1875.

this account progress with that peculiar "looping" movement which strikes even the uninitiated. This group, which is very small, is however the only one which can be founded on the morphology of the larvæ; it comprises only two nearly related families (*Phytometridæ* and *Dendrometridæ*), and it is not yet decided whether these should not be united into one group comprising the family characters of the whole of the "loopers."

Neither the group of Micro-lepidoptera, nor those of the *Noctuina*, *Bombycina*, *Sphingina*, and *Rhopalocera*, can be based systematically on larval characters. Several of these groups are indeed but indistinctly defined, and even the imagines present no common characteristics by which the groups can be sharply distinguished.

This is well shown by the *Rhopalocera* or butterflies. These insects, in their large and generally brilliantly coloured wings, which are usually held erect when at rest, and in their clubbed antennæ, possess characters which are nowhere else found associated together, and which thus serve to constitute them a sharply defined group.<sup>2</sup> The caterpillars, however, show a quite different state

<sup>2</sup> [Lepidopterists are of course aware that even these distinctions are not absolute, as no single character can be named which does not also appear in certain moths. The definition in this case, as in that of most other groups of animals and plants, is only a general one. See, for instance, Westwood's "Introduction to the Classification of Insects," vol. ii. pp. 330—332. Also some remarks by C. V. Riley in his "Eighth

of affairs. Although the larval structure is so characteristic in the individual families of butterflies, these "larval-families" cannot be united into a larger group by any common characters, and the "*Rhopalocera*" would never have been established if only the larvæ had been known. It is true that they all have sixteen legs, that they never possess a Sphinx-like horn, and that they are seldom hairy, as is the case with many *Bombycidae*,<sup>3</sup> but these common *negative* characters occur also in quite distinct groups.

In the butterflies, therefore, a perfect congruence of form-relationship does not exist, inasmuch as the imagines constitute one large group of higher order whilst the larvæ can only be formed into families. If it be admitted that the common characters of butterflies depend on their derivation from a common ancestor, the imagines must have retained certain common characters which enable them to be recognized as allies, whilst the larvæ have preserved no such characters from the period at which the families diverged.

Without going at present into the causes of these phenomena I will pass on to the considera-

Annual Report" on the insects of Missouri, 1876, p. 170. With reference to the antennæ as a distinguishing character, see Mr. A. G. Butler's article in "Science for All," 1880, part xxvii. p. 65. R.M.]

<sup>3</sup> The genus of *Morphinæ*, *Discophora*, possesses hairs very similar to those of the genus *Cnethocampa* belonging to the *Geometræ*.



tion of further facts, and will now proceed to investigate both the form-relationships within the families. Here there can be no doubt that in an overwhelmingly large majority of cases the phyletic development has proceeded with very close parallelism in both stages; larval and imaginal families agree almost completely.

Thus, under the group *Rhopalocera* there is a series of families which equally well permit of their being founded on the structure of the larva or on that of the imago, and in which the larvæ and imagines therefore deviate from one another to the same extent. This is the case, for instance, with the families of the *Pieridæ*, *Papilionidæ*, *Danaidæ*, and *Lycænidæ*.

But there are also families of which the limits would be very different if the larvæ were made the basis of the classification instead of the butterflies as heretofore. To this category belongs the subfamily *Nymphalinx*. Here also a very characteristic form of caterpillar indeed prevails, but it does not occur in all the genera, being replaced in some by a quite different form of larva.

In the latest catalogue of Diurnal Lepidoptera, that of Kirby (1871), 112 genera are comprised under this family. Of these most of the larvæ possess one or several rows of spines on most or on all the segments, a character which, as thus disposed, is not met with in any other family,

This character is noticeable in genera 1 to 90,

if, from those genera of which the larvæ are known, we may draw a conclusion with reference to their allies. I am acquainted with larvæ of genus 2, *Agraulis*, Boisd. (*Dione*, Hübn.); of genus 3, *Cethosia*, Fabr.; 10, *Atella*, Doubl.; 12, *Argynnis*, Fabr.; 13, *Melitæa*,<sup>4</sup> Fabr.; 19, *Araschnia*, Hübn.; 22, *Vanessa*, Fabr.; 23, *Pyrameis*, Hübn.; 24, *Junonia*, Hübn.; 31, *Ergolis*, Boisd.; 65, *Hypolimnas*, Hübn. (*Diadema*, Boisd.); 77, *Limenitis*, Fabr.; 81, *Neptis*, Fabr.; 82, *Athyma*, Westw.; and finally with those of genus 90, *Euthalia*, Hübn.—which, according to Horsfield's figures, possess only two rows of spines, these being re-

<sup>4</sup> [The larvæ of genera 14, *Phyciodes*, and 35, *Crenis*, are likewise spiny. See Edwards' "Butt. of N. Amer." vol. ii. for figures of the caterpillar of *Phyc. Tharos*; for notes on the larvæ of *Crenis Natalensis* and *C. Boisduvali* see a paper by W. D. Gooch, "Entomologist," vol. xiv. p. 36. The larvæ of genus 55, *Ageronia*, are also spiny. (See Burmeister's figure of *A. Arethusa*, "Lép. Rép. Arg." Pl. V. Fig. 4). The larvæ of genus 98, *Aganisthos*, also appear to be somewhat spiny (see Burmeister's figure of *A. Orion*, *loc. cit.* Pl. V. Fig. 6), and this raises the question as to whether the genus is correctly located in its present position. The larvæ of the following genera figured in Moore's "Lepidoptera of Ceylon," parts i. and ii., are all spiny:—6, *Cirrochroa* (Pl. XXXII.); 7, *Cynthia* (Pl. XXVI.); 27, *Kallima* (Pl. XIX.); and 74, *Parthenos* (Pl. XXIV). Many species of caterpillars which are spiny when adult appear to be spineless, or only slightly hairy when young. See Edwards' figures of *Melitæa Phaeton*, *Argynnis Diana*, and *Phyc. Tharos* (*loc. cit.*) and his description of the larva of *Arg. Cybele*, "Canad. Entom." vol. xii. p. 141. The spiny covering thus appears to be a character acquired at a comparatively recent period in the phyletic development. R.M.]

markably long and curved, and fringing both sides. It may be safely assumed that the intermediate genera would agree in possessing this important character of the Nymphalideous larvæ, viz., spines.

After the genus 90 there are 22 more genera, and these are spineless, at least in the case of the two chief genera, 93, *Apatura*, and 104, *Nymphalis*. Of the remainder I know neither figures nor descriptions.\* In the two genera named the larvæ are provided with two or more spine-like tentacles on the head, and the last segment ends in a fork-like process directed backwards. The body is otherwise smooth, and differs also in form from that of the larvæ of the other *Nymphalinae*, being thickest in the middle, and tapering anteriorly and posteriorly; neither is the form cylindrical, but somewhat flattened and slug-shaped. If therefore we were to arrange these butterflies by the larvæ instead of by the imagines, these two genera and their allies would form a distinct family, and could not remain associated with the 90 other Nymphalideous genera.

We have here a case of *incongruence*; the

\* [The larvæ of the 110th genus, *Paphia*, Fabr. (*Anæa*, Hübn.) are also smoothed-skinned. See Edwards' figure (*loc. cit.* vol. i. Pl. XLVI.) of *P. Glycerium*. Also C. V. Riley's "Second Annual Report" on the insects of Missouri, 1870, p. 125. Burmeister figures the larva of a species of *Prepona* (genus 99) which is smooth (*P. Demophon*, *loc. cit.* Pl. V. Fig. 1). The horns on the head of *Apatura*, &c., may possibly be a survival from a former spiny condition. R.M.]

imagines of the genera 1—90 and 91—112 are more closely allied than their larvæ.

From still another side there arises a similar disagreement. The larvæ of the genera *Apatura* and *Nymphalis* agree very closely in their bodily form and in their forked caudal appendage with the caterpillars of another sub-family of butterflies, the *Satyrinæ*, whilst their imagines differ chiefly from those of the latter sub-family in the absence of an enlargement of certain veins of the forewings, an essential character of the *Satyrinæ*.

This double disagreement has also been noticed by those systematists who have taken the form of the caterpillar into consideration. Thus, Morris<sup>6</sup> attempted to incorporate the genera *Apatura* and *Nymphalis* into the family *Libytheidæ*, placing the latter as transitional from the *Nymphalidæ* to the *Satyridæ*. But although the imagines of the genera *Apatura*, *Nymphalis*, and *Libythea* may be most closely related—as I believe they actually are—the larvæ are widely different, being at least as different as are those of *Apatura* and *Nymphalis* from the remaining *Nymphalinæ*.

Now if we could safely raise *Apatura* and *Nymphalis* into a distinct family—an arrangement which in the estimation of Staudinger<sup>7</sup> is correct—

<sup>6</sup> "Synopsis of the described Lepidoptera of North America." Washington, 1862.

<sup>7</sup> "Catalog der Lepidopteren des Europäischen Faunengebietes." Dresden, 1871.



and if this were interpolated between the *Satyridæ* and *Nymphalidæ*, such an arrangement could only be based on the larval structure, and that of the imagines would thus remain unconsidered, since no other common characters can be found for these two genera than those which they possess in common with the other Nymphalideous genera.

The emperor-butterflies (*Apatura*), by the ocelli of their fore-wings certainly put us somewhat in mind of the *Satyrinæ*, in which such spots are always present; but this character does not occur in the genus *Nymphalis*, and is likewise absent in most of the other genera of this group. The genus *Apatura* shows in addition a most striking similarity in the markings of the wings to the purely Nymphalideous genus *Limenitis*, and it is therefore placed, by those systematists who leave this genus in the same family, in the closest proximity to *Limenitis*. This resemblance cannot depend upon mimicry, since not only one or another but *all* the species of the two genera possess a similar marking; and further, because similarity of marking alone does not constitute mimicry, but a resemblance in colour must also be added. The genus *Limenitis* actually contains a case of imitation, but in quite another direction; this will be treated of subsequently.

It cannot therefore be well denied that in this case the larvæ show different relationships to the imagines.

If the "natural" system is the expression of the genetic relationship of living forms, the question arises in this and in similar cases as to whether the more credence is to be attached to the larvæ or to the imagines—or, in more scientific phraseology, which of the two inherited classes of characters have been the most distinctly and completely preserved, and which of these, through its form-relationship, admits of the most distinct recognition of the blood-relationship, or, inversely, which has diverged the most widely from the ancestral form? The decision in single instances cannot but be difficult, and appears indeed at first sight impossible; nevertheless this will be arrived at in most cases as soon as the ontogeny of the larvæ, and therewith a portion of the phylogeny of this stage, can be accurately ascertained.

As in the *Rhopalocera* most of the families show a complete congruence in the form-relationship of the caterpillars and perfect insects, so a similar congruence is also found in the majority of the families belonging to other groups. Thus, the two allied families of the group *Sphingina* can also be very well characterized by their larvæ;<sup>8</sup> both the

<sup>8</sup> This group of moths ("Schwärmer") is regarded as of very different extents by systematists; when I here comprise under it only the *Sphingidæ* proper and the *Sesiidæ*, I by no means ignore the grounds which favour a greater extension of the group; the latter is not rigidly limited. [The affinities of the *Sesiidæ* (*Ægeriidæ*) are by no means clearly made out it

*Sphingidæ* and the *Sesiidæ* possess throughout a characteristic form of larva.

Of the group *Bombycina* the family of the *Saturniidæ* possess thick cylindrical caterpillars, of which the segments are beset with a certain number of knob-like warts. It is true that two genera of this family (*Endromis* and *Aglia*) are without these characteristic warts, but the imagines of these genera also show extensive and common differences from those of the other genera. A distinct family has in fact already been based on these genera (*Endromidæ*, Boisd.). Thus the congruence is not thereby disturbed.

So also the families *Liparidæ*, *Euprepiidæ*, and *Lithosiidæ* appear sharply defined in both forms; and similar families occur likewise under the *Noctuina*, although in this group the erection of families presents great difficulties owing to the near relationship of the genera, and is always to some extent arbitrary. It is important, however, that it is precisely the transitional families which present intermediate forms both as larvæ and as imagines.

Such an instance is offered by the *Acronyctidæ*, a family belonging to the group *Noctuina*. The imagines here show in certain points an approximation to the group *Bombycina*; and their larvæ, which are thickly covered with hairs, likewise

appears probable that they are not related to the *Sphingidæ*.  
See note 1, p. 370. R.M.]

possess the characteristics of many of the caterpillars of this group.<sup>9</sup>

A second illustration is furnished by the family *Ophiussidæ*, which is still placed by all systematists under the *Noctuina*, its affinity to the *Geometrina*, however, being represented by its being located at the end of the *Noctuina*. The broad wings and narrow bodies of these moths remind us in fact of the appearance of the "geometers;" and the larvæ, like the imagines, show a striking resemblance to those of the *Geometrina* in the absence of the anterior abdominal legs. For this reason Hübner in his work on caterpillars has termed the species of this family "*Semi-Geometræ*."

All these cases show a complete congruence in the two kinds of form-relationship; but exceptions are not wanting. Thus, the family *Bombycidæ* would certainly never have been formed if the larval structure only had been taken into consideration, since, whilst the genera *Gastropacha*, *Clisiocampa*, *Lasiocampa*, *Odonestis*, and their allies, are thickly covered with short silky hairs disposed in a very characteristic manner, the caterpillars of the genus *Bombyx*, to which the common silkworm, *B. Mori*, belongs, are quite naked and similar to many Sphinx-caterpillars (*Chærocampa*). Are the imagines of the genera united under this

<sup>9</sup> [For Mr. A. G. Butler's observations on the genus *Acronycta*, see "Trans. Ent. Soc." 1879, p. 313; and note 3, p. 169, of the present volume. R.M.]



family, at any rate morphologically, as unequally related as their larvæ? Whether it is correct to combine them into one family is a question that does not belong here; we are now only concerned with the fact that the two stages are related in form in very different degrees.

An especially striking case of incongruence is offered by the family *Notodontidæ*, under which Boisduval, depending only on imaginal characters, united genera of which the larvæ differed to a very great extent. In O. Wilde's work on caterpillars this family is on this account quite correctly characterized as follows:—"Larvæ of various forms, naked or with thin hairs, sixteen or fourteen legs."<sup>10</sup> In fact in the whole order Lepidoptera there can scarcely be found associated together such diverse larvæ as are here placed in one imago-family; on one side the short cylindrical caterpillars of the genus *Cnethocampa*, Steph. (*C. Processionea*, *Pithyocampa*, &c.), which are covered with fine, brittle, hooked hairs, and are very similar to the

<sup>10</sup> [The following characters are given in Stainton's "Manual of British Butterflies and Moths," vol. i. p. 114:—"Larva of very variable form: at one extreme we find the singular *Cerura* larvæ, with only fourteen legs, and two long projecting tails from the last segment; at the other extreme we have larvæ with sixteen legs and no peculiarity of form, such as *Chaonia* and *Bucephala*; most have, however, the peculiarity of holding the hind segment of the body erect when in repose; generally quite naked, though downy in *Bucephala* and rather hairy in *Curtulu*: very frequently there are projections on the back of the twelfth segment." R.M.]

larvæ of *Gastropacha* with which they were formerly united ; and on the other side there are the naked, humped, and flat-headed larvæ of the genus *Harpyia*, Ochs., with their two long forked appendages replacing the hindmost pair of legs, and the grotesquely formed caterpillars of the genera *Stauropus*, Germ., *Hybocampa*, Linn., and *Noto-donta*, Ochs.

The morphological congruence between larvæ and imagines declares itself most sharply in genera, where it is the rule almost without exception. In this case we can indeed be sure that a genus or sub-genus founded on the imagines only will, in accordance with correct principles, present a corresponding difference in the larvæ. Had the latter been known first we should have been led to construct the same genera as those which are now established on the structure of the imagines, and these, through other circumstances, would have stood in the same degree of morphological relationship as the genera founded on the imagines. There is therefore a congruence in a double sense ; in the first place the differences between the larvæ and imagines of any two genera are equally great, and, in the next place, the common characters possessed by these two stages combined cause them to form precisely the same groups defined with equal sharpness ; the genera coincide completely.

So also the butterflies of the sub-family *Nymphalinae* can well be separated into genera by the

characters of the larvæ, and these, as far as I am able to judge, would agree with the genera founded on the imagines.

The genus *Melitæa*, for example, can be characterized by the possession of 7—9 fleshy tubercles bearing hairy spines; the genus *Argynnis* may be distinguished by always having six hairy unbranched spines on each segment, and the genus *Cethosia* by two similar spines on each segment; the genus *Vanessa* shows sometimes as many as seven branched spines; and the genus *Limenitis* never more than two branched blunt spines on each segment, and so forth. If we go further into details it will be seen that the most closely related imagines, as might indeed have been expected, likewise possess the most nearly allied larvæ, whilst very small differences between the imagines are also generally represented by corresponding differences in the larvæ. Thus, for instance, the genus *Vanessa* of Fabricius has been divided into several genera by later authors. Of these subgenera, *Grapta*, Doubl. (containing the European *C.-album*, the American *Fabricii*, *Interrogationis*, *Faunus*, *Comma*, &c.), is distinguished by the fact that the larvæ not only possess branched spines on all the segments with the exception of the prothorax, but these spines are also present on the head; in the genus *Vanessa* (*sensu strictiori*), Doubl., the head and prothorax are spineless (*e.g.* *V. Urticæ*); in the tropical genus *Junonia*, Hübn.,

which was also formerly (Godart, 1819<sup>11</sup>) united with *Vanessa*, the larvæ bear branched spines on all the segments, the head and prothorax included.

It is possible to go still further and to separate two species of *Vanessa* as two new genera, although they have hitherto been preserved from this fate even by the systematists most given to "splitting." This decision is certainly justifiable, simply because these species at present stand quite alone, and the practical necessity of forming a distinct genus does not make itself felt, and this practical necessity moreover frequently comes into conflict with scientific claims: science erects a new genus based on the amount of morphological difference, it being quite immaterial whether one or many species make up this genus; such an excessive subdivision is, however, a hindrance to practical requirements, as the cumbrous array of names thereby becomes still further augmented.

The two species which I might separate from *Vanessa* on the ground of their greater divergence, are the very common and widely distributed *V. Io* and *Antiopa*, the Peacock Butterfly and the Camberwell Beauty. In the very remarkable pattern of their wings, both show most marked characteristics; *Io* possesses a large ocellus on each wing, and *Antiopa* has a broad light yellow border which is not found in any other species of

<sup>11</sup> Encycl. Meth. ix. p. 310.



*Vanessa*. There can be no doubt but that each of these would have been long ago raised into a genus if similarly marked species of *Vanessa* occurred in other parts of the world, as is the case with the other species of the genus. Thus, it is well known that there is a whole series of species resembling our *V. Cardui*, and another series resembling our *V. C.-album*, the two series possessing the same respective types of marking; indeed on these grounds the sub-genera *Pyrameis* and *Grapta* have been erected.<sup>12</sup>

I should not have considered it worth while to have made these remarks if it had not been for the fact that the caterpillars of *V. Io* and *V. Antiopa* differ in small particulars from one another and from the other species of the genus. These differences relate to the number and position of the spines, as can be seen from the following table:—

<sup>12</sup> [The genus *Vanessa* (in the wide sense) appears to be in a remarkable condition of what may be called phyletic preservation. Thus, the group of species allied to *V. C.-album* passes by almost insensible steps into the group of butterflies typified by our "Tortoiseshells." The following is a list of some of the intermediate species in their transitional order:—*I.-album*, *V.-album*, *Faunus*, *Comma*, *Californica*, *Dryas*, *Polychloros*, *Xanthomelas*, *Cashmirensis*, *Urticæ*, *Milberti*, &c. Similarly, our *Atalanta* and *Cardui* are connected by a number of intermediate forms, showing a complete transition from the one to the other. The following is the order of the species so far as I am acquainted with them:—*Atalanta*, *Dejeanii*, *Callirhoë*, *Tammeamea*, *Myrinna*, *Huntera*, *Terpsichore*, *Carye*, *Kershawii*, and *Cardui*. R.M.]

SPECIES OF THE GENUS *VANESSA*, FABR.

	Number of Spines on the head and segments of the larva.							
	Head.	Segm. I.	Segm. II.	Segm. III.	Segm. IV.	Segm. V.	Segm. VI.—XI.	Segm. XII.
V. Io . . . .	0	0	2	2	4	6	6	4
V. Antiopa . .	0	0	4	4	6	6	7	4
V. Urticæ . . .	0	0	4	4	7	7	7	4
V. Polychloros .	0	0	4	4	7	7	7	4
V. Ichnusa . . .	0	0	4	4	7	7	7	4
V. Atalanta . .	0	0	4	4	7	7	7	4
V. C.-album . .	2	0	4	4	7	7	7	4
V. Interrogationis	2	0	4	4	7	7	7	4
V. Levana . . .	2	0	4	4	7	7	7	4

This character of the number of spines will not be considered as too unimportant when we observe how perfectly constant it remains in the nearly allied species. This is the case in the three consecutive forms, *Urticæ*, *Polychloros*, and *Ichnusa*. Now when we see that two species which differ in their imaginal characters present correspondingly small differences in their larvæ, this exact systematic congruence indicates a completely parallel phyletic development.

Exceptions are, however, to be met with here. Thus, Hübner has united one group of the species

of *Vanessa* into the genus *Pyrameis* just mentioned, on account of certain characteristic distinctions of the butterflies. I do not know, however, how this genus admits of being grounded on the structure of the larvæ; the latter, as appears from the above table, agree exactly in the number and position of the spines with the caterpillars of *Vanessa* (*sensû strictiori*), nor can any common form of marking be detected which would enable them to be separated from *Vanessa*.

Still more striking is the incongruence in the genus *Araschnia*, Hübn. (*A. Prorsa-Levana*), which, like the genus *Pyrameis*, is entirely based on imaginal characters. This is distinguished from all the other sub-genera of the old genus *Vanessa* by a small difference in the venation of the wings (the discoidal cell of the hind-wings is open instead of closed). Now it is well-known that in butterflies the wing-venation, as most correctly shown by Herrich-Schäffer, is the safest criterion of "relationship." It thus happens that this genus, typified by the common *Levana*, is in Kirby's Catalogue separated from *Vanessa* by two genera, and according to Herrich-Schäffer<sup>13</sup> by forty genera! Nevertheless, the larvæ agree so exactly in their spinal formula with *Grapta* that we should have no hesitation in regarding them as a species of this sub-genus. It appears to me

<sup>13</sup> "Prodromus Systematis Lepidopterorum." Regensburg, 1864.

very probable that in this case the form-relationship of the caterpillar gives more correct information as to the blood-relationship of the species than that of the imago—in any case the larvæ show a different form-relationship to the imagines.

Just as in the case of butterflies there are many genera of *Sphingidæ* which can be based on the structure of the larvæ, and which agree with those founded on the imagines.

Thus, the genus *Macroglossa* is characterized by a straight anal horn, a spherical head, and by a marking composed of longitudinal stripes, these characters not occurring elsewhere in this combination. The nearly allied genus *Pterogon*, on the other hand, cannot be based on the larvæ only, since not only is the marking of the adult larva very distinct in the different species, but the anal horn is present in two species, whilst in a third (*P. Cœnotheræ*) it is replaced by a knob-like eye-spot. The genus *Sphinx* (*sensû strictiori*) is distinguished by the simple, curved caudal horn, the smooth, egg-shaped head and smooth skin, and by a marking mainly composed of seven oblique stripes. The genus *Deilephila* is distinguished from the preceding by a dorsal plate, situated on the prothorax and interrupting the marking, as well as by the pattern, which here consists of a subdorsal line with ring-spots more or less numerous and developed; the skin also is rough,



"shagreened," although it must be admitted that there are exceptions (*Vespertilio*). The genus *Charocampa* admits also of being based on the form-relationship of its caterpillars, although this is certainly only possible by disregarding the marking and taking alone into consideration the peculiar pig-like form of the larvæ. The genus *Acherontia*, so nearly related to *Sphinx*, possesses in the doubly curved caudal horn a character common to the genus (three species known<sup>14</sup>). Finally may be mentioned the genus *Smerinthus*, of which the larvæ, by their anteriorly tapering form, their shagreened skin and almost triangular head with the apex upwards, their simply curved anal horn, and by their seven oblique stripes on each side, constitute a genus as sharply defined as that formed by the moths.

Although in all the systematic divisions hitherto treated of there are cases where the form-relationship of the larva does not completely coincide with that of the imago, such incongruences are of far more frequent occurrence in the smallest systematic group, viz. species.

The larvæ of two species have very frequently a much nearer form-relationship than their imagines. Thus, the caterpillars of *Smerinthus*

<sup>14</sup> [The larva of *Acherontia Morda*, figured by Butler (see note 50, p. 262), possesses the characteristically recurved horn; that of *Ach. Medusa* figured by the same author, does not appear to possess this character in any marked degree. R.M.]

*Ocellatus* and *S. Populi* are closely allied in structure, marking, and colouring, whilst the moths in these two last characters and in the form of the wings are widely separated.<sup>15</sup> Judging from the larvæ we should expect to obtain two very similar moths, but in fact both *Populi* and *Ocellatus* have many near allies, and these closely related species sometimes possess larvæ which differ more widely than those of more distantly related species of imagines.

Thus, in Amur-land and North America there occur species of *Smerinthus* which closely resemble our *Ocellatus* in colour, marking, and form of wing, and which possess the characteristic large blue ocellus on the hind-wings. *S. Excacatus* is quite correctly regarded as the representative American form of our *Ocellatus*, but its caterpillar, instead of being leaf-green, is of a chrome-yellow, and possesses dark green instead of white oblique stripes, and has moreover a number of red spots, and a red band on the head—in brief, in the very characters (colour and certain of the markings) in which the imagines completely agree it is widely different from *Ocellatus*. It appears also to be covered with short bristles, judging from Abbot and Smith's figure.<sup>16</sup>

Just in the same way that the species having

<sup>15</sup> [See note 28, p. 233. R.M.]

<sup>16</sup> *Loc. cit.* Pl. XXV. [This species is referred by Butler to the genus *Paonias*, Hübn. R.M.]

the nearest conceivable form-relationship to *Ocellatus* possesses a relatively strongly diverging larva, so does the nearest form-relation of *Populi* (imago) offer a parallel case. This species, which is also North American, lives on *Juglans Alba*. The imago of *Smerinthus Juglandis* differs considerably from *S. Populi* in the form of the wings, but it resembles the European species so closely in marking and colouring that no doubt can exist as to the near relationship of the two forms. The caterpillar of *S. Juglandis*,<sup>17</sup> however, differs to a great extent from that of *Populi* in colour—it is not possible to confound these two larvæ; but those of *Populi* and *Ocellatus* are not only easily mistaken for one another, but are distinguished with difficulty even by experts.

In this same family of the *Sphingidæ* cases are not wanting in which, on the other hand, the moths are far more closely allied than the larvæ.

<sup>17</sup> Abbot and Smith, Pl. XXIX. [Placed by Butler in the genus *Cressonia*, Grote and Robinson. Abbot and Smith state that this larva is sometimes green. According to Mr. Herman Strecker (Lepidop. Rhopal. and Hetero, Reading, Pa. 1874, p. 54) it feeds upon black walnut (*Juglans Nigra*), hickory (*Carya Alba*), and ironwood (*Ostrya Virginica*). Of the North American species of *Smerinthus*, the following, in addition to *Excæcatus*, closely resemble our *Ocellatus*:—*S. (Calasymbolus) Geminatus*, Say; (*C.*) *Cerisii*, Kirby; and *Ophthalmicus*, Boisd. In addition to *S. (Cressonia) Juglandis*, *S. (Triptogon) Modesta* much resembles our *Populi*. The larva of *Geminatus*, according to Strecker, is "pale green, lightest above, with yellow lateral granulated stripes; caudal horn violet; stigmata red. It feeds on the willow." R.M.]

This is especially striking in the genus *Deilephila*, eight species of which are allied in the imaginal state in a remarkable degree, whilst the larvæ differ greatly from one another in colour, and to as great an extent in marking. These eight species are *D. Nicæa*, *Euphorbiæ*, *Dahlii*, *Galii*, *Livornica*, *Lineata*, *Zygophylli*, and *Hippophaës*. Of these, *Nicæa*, *Euphorbiæ*, *Dahlii*, *Zygophylli*, and *Hippophaës* are so much alike in their whole structure, in the form of the wings, and in marking, that few entomologists can correctly identify them off-hand without comparison. The larvæ of these four species, however, are of very different appearances. Those of *Euphorbiæ* and *Dahlii* are most alike, both being distinguished by the possession of a double row of large ring-spots. *Zygophylli* (see Fig. 50, Pl. VI.) possesses only faint indications of ring-spots on a white subdorsal line; and in *Hippophaës* there is only an orange-red spot on the eleventh segment, the entire marking consisting of a subdorsal line on which, in some individuals, there are situated more or less developed ring-spots (see Figs. 59 and 60, Pl. VII). If we only compare the larvæ and imagines of *D. Euphorbiæ* and *Hippophaës*, we cannot but be struck with astonishment at the great difference of form-relationship in the two stages of development.

In the case of *D. Euphorbiæ* and *Nicæa* this difference is almost greater. Whilst these larvæ show great differences in colour, marking, and in



the roughness or smoothness of the skin (compare Fig. 51, Pl. VI. with Figs. 43 and 44, Pl. V.), the moths cannot be distinguished with certainty. As has already been stated, the imago of the rare *D. Nicæa* is for this reason wanting in most collections; it cannot be detected whether a specimen is genuine, *i. e.* whether it may not perhaps be a somewhat large example of *D. Euphorbiæ*.

An especially striking instance of incongruence is offered by the two species of *Chærocampa* most common with us, viz., *Elpenor* and *Porcellus*, the large and small Elephant Hawk-moths. The larvæ are so similar, even in the smallest details of marking, that they could scarcely be identified with certainty were it not that one species (*Elpenor*) is considerably larger and possesses a less curved caudal horn than the other. The moths of these two species much resemble one another in their dull green and red colours, but differ in the arrangement of these colours, *i. e.* in marking, and also in the form of their wings, to such an extent that *Porcellus* has been referred to the genus *Pergesa*<sup>18</sup> of Walker. If systemy, as is admitted on many sides, has only to indicate the morphological relationship, this author is not to blame—but in this case a special larval classification must likewise be admitted, in a manner somewhat similar to that at present adopted provisionally in text-books of zoology for the

<sup>18</sup> Cat. Brit. Mus.

Hydroid Polypes and inferior Medusæ. This case of *Porcellus*, however, shows that those are correct who maintain that systemy claims to express, although incompletely, the blood-relationship, and that systematists have always unconsciously formed their groups as though they intended to express the genetic connection of the forms. Only on this supposition can it appear incorrect to us to thus separate two species of which the larvæ agree so completely.

I cannot conclude this review of the various systematic groups without taking a glance at the groups comprised within species, viz. varieties. Whilst in species incongruence is of frequent occurrence, in varieties this is the rule, for which reason it admits in this case of being more sharply defined, since we are not concerned with a double difference but only with the question whether in the one stage a difference or an absolute similarity is observable. By far the majority of varieties are either simply imaginal or merely larval varieties—only the one stage diverges, the other is quite constant.

Thus, as has already been shown, in all the seasonally dimorphic butterflies known to me the caterpillars of the two generations of imagines, which are often so widely different, are exactly alike; and the same obtains for the majority of purely climatic varieties of butterflies. Unfortunately there are as yet no connected observa-

tions on this point. The only certain instance that I can here mention is that of the Alpine and Polar form of *Pieris Napi*. This variety, *Bryoniæ*, the female of which differs so greatly in marking and colouring, possesses larvæ which cannot be distinguished from those of the ordinary form of *Napi*. (See part I. appendix I. p. 124.)

That caterpillars can also vary locally without thereby affecting the imagines is shown by the frequently mentioned and closely investigated cases of di- and polymorphism in the larvæ of a number of *Sphingidæ* (*M. Stellatarum*, *A. Atropos*, *S. Convolvuli*, *C. Elpenor*, and *Porcellus*, &c.). The same thing is still more clearly shown by those instances in which there are not several but only one distinct larval form occurring in each of two different localities.

To this class belongs the above-mentioned case of *Chærocampa Celerio* (p. 197), supposing our information concerning this species to be correct; likewise the recently-mentioned case of the Ligurian variety of the caterpillar of *Saturnia Carpini*; and finally the case of *Eriogaster Lanes-tris*, so well known to lepidopterists. This insect inhabits the plains of Germany, and in the Alps extends to an elevation of 7000 feet, where it possesses a larva differently marked and coloured (*E. Arbusculæ*) to those of the lowlands whilst the moths are smaller, but do not differ in other respects from those of the plains.

Among the Alpine species many other such cases may occur, but these could only be discovered by making investigations having special reference to this point. Of the Alpine butterflies, for example, not a single species can have been reared from the caterpillar ; for this reason but few observations have on the whole been given by entomologists respecting the Alpine larvæ, which are not known sufficiently well to enable such a question to be decided.

The investigation of the form-relationships existing between larvæ on the one hand and imagines on the other has thus led to the following results :—

We learn on comparison that incongruences or inequalities of form-relationship occur in all systematic groups from varieties to families. These incongruences are of two kinds, in some cases being disclosed by the fact that the larvæ of two systematic groups, *e. g.* two species, are more closely related in form than their imagines (or inversely), whilst in other cases the larvæ form different systematic groups to those formed by the imagines.

The results of the investigation into the occurrence of incongruences among the various systematic groups may be thus briefly summarised :—

Incongruences appear to occur most frequently among varieties, since it very frequently happens that it is only the larva or only the imago which



has diverged into a variety, the other stage remaining monomorphic. The systematic division of varieties is thus very often one-sided.

Among species also incongruences are of frequent occurrence. Sometimes the imagines are much more nearly related in form than the larvæ, and at others the reverse happens; whilst again the case appears also to occur in which only the one stage (larva) diverges to the extent of specific difference, the other stage remaining monomorphic (*D. Euphorbiæ* and *Nicæa*).

The agreement in form-relationship appears to be most complete in genera. In the greater number of cases the larval and imaginal genera coincide, not only in the sharpness of their limits, but also—as far as one can judge—in the weight of their distinctive characters, and therefore in the amount of their divergence. Of all the systematic groups, genera show the greatest congruence.

In families there is again an increase of irregularity. Although larval and imaginal families generally agree, there are so many exceptions that the groups would be smaller if they were based exclusively on the larval structure than if founded entirely on the imagines (*Nymphalidæ*, *Bombycidæ*).

If we turn to the groups of families we find a considerably increased incongruence; complete agreement is here again rather the exception, and it further happens in these cases that it is always

the larvæ which, to a certain extent, remain at a lower grade, and which form well defined families ; but these can seldom be associated into groups of a higher order having a common character, as in the case of the imagines (*Rhopalocera*).

After having thus collected (so far as I am able) the facts, we have now to attempt their interpretation, and from the observed congruence and incongruence of form-relationship of the two stages to endeavour to draw a conclusion as to the underlying causes of the transformations.

It is clear at starting that all cases of incongruence can only be the expression or the consequence of a phyletic development which has not been exactly parallel in the two stages of larva and imago—that one stage must have changed either more rapidly or more slowly than the other. An “unequal phyletic development” is thus the immediate cause of incongruence.

Thus, the occurrence of different larvæ in species of which the imagines have remained alike may be simply understood as cases in which the imago only has experienced a change—has taken a forward step in phyletic development, whilst the larvæ have remained behind. If we conceive this one-sided development to be repeated several times, there would arise two larval forms as widely different as those of *Deilephila Nicæa*, and *Euphorbia*, whilst the imagines, as is actually the case in these species, would remain the same.

The more commonly occurring case in which one stage has a greater form-divergence than the other, is explicable by the one stage having changed more frequently or more strongly than the other.

The explanation of the phenomena thus far lies on the surface, and it is scarcely possible to advance any other; but why should one stage become changed more frequently or to a greater extent than the other? why should one portion be induced to change more frequently or more strongly than another? whence come these inducements to change? These questions bring us to the main point of inquiry:—Are the causes which give rise to these changes internal or external? Are the latter the result of a phyletic vital force, or are they only due to the action of the external conditions of life?

Although an answer to this question will be found in the preceding essay, I will not support myself on the results there obtained, but will endeavour to give another solution of the problem on fresh grounds. The answer will indeed be the same as before:—A phyletic force must be discountenanced, since in the first place it does not explain the phenomena, and in the second place the phenomena can be well explained without its assumption.

The admission of a phyletic vital force does not explain the phenomena. The assumption that there is a transforming power innate in the organ-

ism indeed agrees quite well with the phenomenon of congruence, but not with that of incongruence. Since a large number of cases of the latter depend upon the fact that the larvæ are more frequently influenced by causes of change than their imagines, or *vice versâ*, how can this be reconciled with such an internal force? On this assumption would not each stage of a species be compelled to change, if not contemporaneously at least successively, with the same frequency and intensity, by the action of an innate force? and how by means of the latter can there ever result a greater form-divergence in the larvæ than in the imagines?

It is delusive to believe that these unequal deviations can be explained by assuming that the phyletic force acts periodically. Granting that it does so, and that the internal power successively compels the imago, pupa, and finally the larva to change, there would then pass a kind of wave of transformation over the different stages of the species, as was actually shown above to be the case in the single larval stages. The only possible way of explaining the unequal distances between larvæ and imagines would therefore be to assume that two allied groups, *e. g.* species, were not contemporaneously affected by the wave, so that at a certain period of time the imago alone of one species had become changed, whilst in the other species the wave of transformation had also reached the larva. In this case the imagines of the two



species would thus appear to be more nearly related than their larvæ.

Now this strained explanation is eminently inapplicable to varieties, still less to species, and least of all to higher systematic groups, for the simple reason that every wave of transformation may be assumed to be at the most of such strength as to produce a deviation of form equal to that of a variety. Were the change resulting from a single disturbance greater, we should not only find one-sided varieties, *i. e.* those belonging to *one* stage, but we should also meet as frequently with one-sided species. If, however, a wave of transformation can only produce a variety even in the case of greatest form-divergence, the above hypothetical untemporaneous action of such a wave in two species could only give rise to such small differences in the two stages that we could but designate them as varieties. An accumulation of the results of the action of several successive waves passing over the same species could not happen, because the distance from a neighbouring species would always become the same in two stages as soon as *one* wave had ended its course. In this manner there could therefore only arise divergences of the value of varieties, and incongruences in systematic groups of a higher rank could not thus be explained.

All explanations of the second form of incongruence from the point of view of a phyletic force

can also be shown to be absurd. How can the fact be explained that larval and imaginal families by no means always coincide; or that the larvæ can only be formed into families whilst the imagines partly form sharply defined groups of a higher order? How can an internal directive force within the same organism urge in two quite distinct directions? If the evolution of a definite system were designed, and the admission of such a continually acting power rendered necessary, why such an incomplete, uncertain, and confused performance?

I must leave others to answer these questions; to me a vital force appears to be inadmissible, not only because we cannot understand the phenomena by its aid, but above all because it is superfluous for their explanation. In accordance with general principles the assumption of an unknown force can, however, only be made when it is indispensable to the comprehension of the phenomena.

I believe that the phenomena can be quite well understood without any such assumption—both the phenomena of congruence and incongruence, in their two forms of unequal divergence and unequal group-formation.

Let us in the first place admit that there is no directive force in the organism inciting periodic change, but that every change is always the consequence of external conditions, being ultimately nothing but the reaction—the *réponse* of the

organism to some of the influences proceeding from the environment; every living form would in this case remain constant so long as it was not compelled to change by inciting causes. Such transforming factors can act directly or indirectly, *i. e.* they can produce new changes immediately, or can bring about a remodelling by the combination, accumulation, or suppression of individual variations already present (adaptation by natural selection). Both forms of this action of external influences have long been shown to be in actual operation, so that no new assumption will be made, but only an attempt to explain the phenomena in question by the sole action of these known factors of species formation.

If, in the first instance, we fix our attention upon that form of incongruence which manifests itself through unequal divergence of form-relationship, it will appear prominently that this bears precise relations to the different systematic groups. This form of incongruence constitutes the rule in varieties of the order Lepidoptera, it is of very frequent occurrence in species, but disappears almost completely in genera, and entirely in the case of families and the higher groups. On the whole, therefore, as we turn to more and more comprehensive groups, the incongruence diminishes whilst the congruence increases, until finally the latter becomes the rule.

Now if congruence presupposes an equal

number of transforming impulses, we perceive that the number of the impulses which have affected larvæ and imagines agree with one another the more closely the larger the systematic groups which are compared together. How can this be otherwise? The larger the systematic group the longer the period of time which must have been necessary for its formation, and the more numerous the transforming impulses which must have acted upon it before its formation was completed.

But if the supposition that the impulse to change always comes from the environment in no way favours the idea that such impulses always affect both stages contemporaneously, and are equal in number during the same period of time, there is not, on the other hand, the least ground for assuming that throughout long periods the larvæ or the imagines only would have been affected by such transforming influences. This could have been inferred from the fact that varieties frequently depend only upon one stage, whilst specific differences in larvæ only also occur occasionally, the imagines remaining alike; but no single genus is known of which all the species possess similar larvæ. Within the period of time during which genera can be formed the transforming impulses therefore never actually affect the one stage only, but always influence both.

But if this is the case—if within the period of



time which is sufficient for the production of species, the one stage only is but seldom and quite exceptionally influenced by transforming impulses, whilst both stages are as a rule affected, although not with the same frequency, it must necessarily follow that on the whole, as the period of time increases, the difference in the number of these impulses which affect the larva and of those which affect the imago must continually decrease, and with this difference the magnitude of the morphological differences resulting from the transforming influences must at the same time also diminish. With the number of the successively increasing changes the difference in the magnitude of the change in the two stages would always relatively diminish until it had quite vanished from our perception; just in the same manner as we can distinguish a group of three grains of corn from one composed of six, but not a heap of 103 grains from one containing 106 grains.

That the small systematic groups must have required a short period and the large groups a long period of time for their formation requires no special proof, but results immediately from the theory of descent.

All the foregoing considerations would, however, only hold good if the transforming impulses were equal in strength, or, not to speak figuratively, if the changes only occurred in equivalent portions of the body, *i. e.* in such portions as those

in which the changes are of the same physiological and morphological importance to the whole organism.

Now in the lower systematic groups this is always the case. Varieties, species, and genera are always distinguished by only relatively small differences; deep-seated distinctions do not here occur, as is implied in the conception of these categories. The true cause of this is, I believe, to be found in the circumstance that all changes take place only by the smallest steps, so that greater differences can only arise in the course of longer periods of time, within which a great number of types (species) can, however, come into existence, and these would be related by blood and in form in different degrees, and would therefore form a systematic group of a higher rank.

The short periods necessary for the production of inferior groups, such as genera, would not result in incongruences if only *untypical* parts of the larvæ, such as marking or spines, underwent change, whilst in the imagines typical parts—wings and legs—became transformed. The changes which could have occurred in the wings, &c., during this period of time would have been much too small to produce any considerable influence on the other parts of the body by correlation; and two species of which the larvæ and imagines, had changed with the same frequency, would show

a similar amount of divergence between the larvæ and between the imagines, although on the one side only *untypical* parts—*i. e.* those of no importance to the whole organization—and on the other side typical parts, were affected. The *number* of the changes would here alone determine whether congruence or incongruence occurred between the two stages.

The case would be quite different if, throughout a long period of time, in the one stage only typical and in the other only untypical parts were subjected to change. In the first case a complete transformation of the whole structure would occur, since not only would the typical parts, such as the wings, undergo a much further and increasing transformation in the same direction, but these changes would also lead to secondary alterations.

In this manner, I believe, must be explained the fact that in the higher groups still greater form-divergences of the two stages occur; and if this explanation is correct, the cause of this striking phenomenon, *viz.*, that incongruence diminishes from varieties to genera, in which latter it occurs but exceptionally, whilst in families and in the higher groups it again continually increases, is likewise revealed. Up to genera the incongruence depends entirely upon the one stage having become changed *more frequently* than the other; but in families and groups of families, and in the

orders Diptera and Hymenoptera, as will be shown subsequently, in sub-orders and tribes, it depends upon the *importance of the part of the body* affected by the predominant change. In the latter case the number of changes is of no importance, because these are so numerous that the difference vanishes from our perception; but an equal number of changes, even when very great, may now produce a much greater or a much smaller transformation in the entire bodily structure according as they affect typical or untypical portions, or according as they keep in the same direction throughout a long period of time, or change their direction frequently.

Those unequal form-divergences which occur in the higher systematic groups are always associated with a different formation of groups—the larvæ form different systematic groups to the imagines, so that one of these stages constitutes a higher or a lower group; or else the groups are of equal importance in the two stages, but are of unequal magnitude—they do not coincide, but the one overlaps the other.

Incongruences of this last kind appear in certain cases within families (*Nymphalidæ*), but I will not now subject these to closer analysis, because their causes will appear more clearly when subsequently considering the orders Hymenoptera and Diptera. Incongruences of the first kind, however, admit of a clear explanation in the case of butterflies.



They appear most distinctly in the groups composed of families.

Nobody has as yet been able to establish the group *Rhopalocera* by means of any single character common to the larvæ; nevertheless, this group in the imagines is the sharpest and best defined of the whole order. If we inform the merest tyro that clubbed antennæ are the chief character of the butterflies, he will never hesitate in assigning one of these insects to its correct group. Such a typical character, common to all families, is, however, absent in the larvæ; and it might be correctly said that there were no Rhopaloceros larvæ, or rather that there were only larvæ of *Equites*, *Nymphales*, and *Heliconii*. The larvæ of the various families can be readily separated by means of characteristic distinctions, and it would not be difficult for an adept to distinguish to this extent in single cases a Rhopaloceros caterpillar as such; but these larvæ possess only *family* characters, and not those of a higher order.

This incongruence partly depends upon the circumstance that the form-divergence between a Rhopaloceros and a Heteroceros family is much greater on the side of the imagines than on that of the larvæ. Were there but a single family of butterflies in existence, such as the *Equites*, we should be obliged to elevate this to the rank of a sub-order on the side of the imagines, but not on

that of the larvæ. Such cases actually occur, and an instance of this kind will be mentioned later in connection with the Diptera. But this alone does not explain why, on the side of the imagines, a whole series of families show the same amount of morphological divergence from the families of other groups. There are two things, therefore, which must here be explained :—First, why is the form-divergence between the imagines of the Rhopalocera and Heterocera greater than that between their larvæ? and, secondly, why can the imagines of the Rhopalocera be formed into one large group by means of common characters whilst the larvæ cannot?

The answers to both these questions can easily be given from our present standpoint. As far as the first question is concerned, this finds its solution in the fact that the form-divergence always corresponds exactly with the divergence of function, *i. e.* with the divergence in the mode of life.

If we compare a butterfly with a moth there can be no doubt that the difference in the conditions of life is far greater on the side of the imagines than on that of the larvæ. The differences in the mode of life of the larvæ are on the whole but very small. They are all vegetable feeders, requiring large quantities of food, and can only cease feeding during a short time, for which reason they never leave their food-plants for long, and it is of more importance for them to remain

firmly attached than to be able to run rapidly. It is unnecessary for them to seek long for their food, as they generally find themselves amidst an abundance, and upon this depends the small development of their eyes and other organs of sense. On the whole caterpillars live under very uniform conditions, although these may vary in manifold details.

The greatest difference in the mode of life which occurs amongst Lepidopterous larvæ is shown by wood feeders. But even these, which by their constant exclusion from light, the hardness of their food, their confinement within narrow hard-walled galleries, and by the peculiar kind of movement necessitated by these galleries, are so differently situated in many particulars to those larvæ which live openly on plants, have not experienced any general change in the typical conformation of the body by adaptation to these conditions of life. These larvæ, which, as has already been mentioned, belong to the most diverse families, are more or less colourless and flattened, and have very strong jaws and small feet ; but in none of them do we find a smaller number of segments, or any disappearance, or important transformation of the typical limbs ; they all without exception possess sixteen legs, like the other larvæ excepting the *Geometræ*.

Now if even under the most widely diverging conditions of life adaptation of form is produced by

relatively small, and to a certain extent superficial, changes, we should expect less typical transformations in the great majority of caterpillars which live on the exterior of plants or in their softer parts (most of the Micro-lepidoptera). The great diversity in the forms of caterpillars depends essentially upon a different formation of the skin and its underlying portions. The skin is sometimes naked, and can then acquire the most diverse colours, either protective or conspicuous, or it may develop offensive or defensive markings; in other cases it may be covered with hairs which sting, or with spines which prick; certain of its glands may develop to an enormous size, and acquire brilliant colours and the power of emitting stinking secretions (the tentacles of the *Papilionidæ* and Cuspidate larvæ); by the development of warts, angles, humps, &c., any species of caterpillar may be invested with the most grotesque shape, the significance of which with respect to the life of the insect is as yet in most cases by no means clear: *typical portions* are not, however, essentially influenced by these manifold variations. At most only the form of the individual segments of the body, and with these the shape of the whole insect, become changed (onisciform larvæ of *Lycænidæ*), but a segment is never suppressed, and even any considerable lengthening of the legs occurs but very seldom (*Stauropus Fagi*).<sup>19</sup>

<sup>19</sup> [This lengthening of the true legs is mimetic according



We may therefore fairly assert that the structure of larvæ is on the whole remarkably uniform, in consequence of the uniformity in the conditions of life. Notwithstanding the great variety of external aspects, the general structure of caterpillars does not become changed—it is only their outward garb which varies, sometimes in one direction, and sometimes in another, and which, starting from inherited characters, becomes adapted to the various special conditions of life in the best possible manner.

All this is quite different in the case of the imagines, where we meet with very important differences in the conditions of life. The butterflies, which live under the influence of direct sunlight and a much higher temperature, and which are on the wing for a much longer period during the day, must evidently be differently equipped to the moths in their motor-organs (wings), degree of hairiness, and in the development of their eyes and other organs of sense. It is true that we are not at present in a condition to furnish special proofs that the individual organs of butterflies are exactly adapted to a diurnal life, but we may safely draw this general conclusion from the circumstance that no butterfly is of nocturnal habits.<sup>20</sup>

to Hermann Müller, and causes the anterior portion of the caterpillar to resemble a spider. See note 1, p. 290. R.M.]

<sup>20</sup> [Certain butterflies appear to be crepuscular, if not nocturnal in their habits. Thus in his "Notes on the Lepidoptera

It cannot be stated in objection that there are many moths which fly by day. It certainly appears that no great structural change is necessary to confer upon a Lepidopteron organized for nocturnal life the power of also flying by day; but this proves nothing against the view that the structure of the butterflies depends upon adaptation to a diurnal life. Analogous cases are known to occur in many other groups of animals. Thus, the decapodous Crustacea are obviously organized for an aquatic life; but there are some crabs which take long journeys by land. Fish appear no less to be exclusively adapted to live in water; nevertheless the "climbing-perch" (*Anabas*) can live for hours on land.

It is not the circumstance that some of the moths fly by day which is extraordinary and demands a special explanation, but the reverse fact just mentioned, that no known butterfly flies by night. We may conclude from this that the organization of the latter is not adapted to a nocturnal life,

If we assume <sup>21</sup> that the Lepidopterous family

of Natal," Mr. W. D. Gooch states that he never saw *Melanitis*, *Leda*, or *Gnophodes Parmeno* on the wing by day, but generally during the hour after sunset. He adds:—"My sugar always attracted them freely, even up to 10 or 11 p.m." Many species of *Hesperidæ* are also stated to be of crepuscular habits by this same observer. See "Entomologist," vol. xvi. pp. 38 and 40. R.M.]

<sup>21</sup> I only make this assumption for the sake of simplicity

adapted to a diurnal life gives rise in the course of time to a nocturnal family, there can be no doubt but that the transformation of structure would be far greater on the part of the imagines than on that of the larvæ. The latter would not remain quite unchanged—not because their imagines had taken to a nocturnal life which for the larva would be quite immaterial, but because this change could only occur very gradually in the course of a large number of generations, and during this long period the conditions of life would necessarily often change with respect to the larvæ. It has been shown above that within the period of time necessary for the formation of a new species impulses to change occur on both sides; how much more numerous therefore must these be in the case of a group of much higher rank, for the establishment of which a considerably longer period is required. In the case assumed, therefore, the larvæ would also change, but they would suffer much smaller transformations than the imagines. Whilst in the latter almost all the typical portions of the body would undergo deep changes in consequence of the entirely different conditions of life, the larvæ would perhaps only change in marking, hairs, bristles, or other external characters, the typical parts experiencing only unimportant modifications.

In this manner it can easily be understood why and not because I am convinced that the existing *Rhopalocera* are actually the oldest Lepidopterous group.

the larvæ of a family of *Noctuæ* do not differ to a greater extent from those of a family of butterflies than do the latter from some other Rhopalocerous family, or why the imagines of a Rhopalocerous and a Heterocerous family present much greater form-divergences than their larvæ. At the same time is therefore explained the unequal value that must be attributed to any single family of butterflies in its larvæ and in its imagines. The unequal form-divergences coincide exactly with the inequalities in the conditions of life.

When whole families of butterflies show the same structure in their typical parts (antennæ, wings, &c.), and, what is of more importance, can be separated as a systematic group of a higher order (*i. e.* as a section or sub-order) from the other Lepidoptera whilst their larval families do not appear to be connected by any common character, the cause of this incongruence lies simply in the circumstance that the imagines live under some peculiar conditions which are common to them all, but which do not recur in other Lepidopterous groups. Their larvæ live in precisely the same manner as those of all the other families of Lepidoptera—they do not differ in their mode of life from those of the Heterocerous families to a greater extent than they do from one another.

We therefore see here a community of form within the same compass as that in which there is community in the conditions of life. In all butter-



flies such community is found in their diurnal habits, and in accordance with this we find that these only, and not their larvæ, can be formed into a group having common characters.

In the larvæ also we only find agreement in the conditions of life within a much wider compass, viz. within the whole order. Between the limits of the order Lepidoptera the conditions of life in the caterpillars are, as has just been shown, on the whole very uniform, and the structure of the larvæ accordingly agrees almost exactly in all Lepidopterous families in every essential, *i. e.* typical, part.

In this way is explained the hitherto incomprehensible phenomenon that the sub-ordinal group *Rhopalocera* cannot be based on the larvæ, but that Lepidopterous caterpillars can as a whole be associated into a higher group (order) ; they constitute altogether families and an order, but not the intermediate group of a sub-order. By this means we at the same time reply to an objection that may be raised, viz. that larval forms cannot be formed into high systematic groups because of their " low and undeveloped " organization.

To this form of incongruence, viz. to the formation of systematic groups of unequal value and magnitude, I must attach the greatest weight with respect to theoretical considerations. I maintain that this, as I have already briefly indicated above, is wholly incompatible with the admission of a phyletic force. How is it conceivable that such a

power could work in the same organism in two entirely different directions—that it should in the same species lead to the constitution of quite different systems for the larvæ and for the imagines, or that it should lead only to the formation of families in the larvæ and to sub-orders in the imagines? If an internal force existed which had a tendency to call into existence certain groups of animal forms of such a nature that these constituted one harmonious whole of which the components bore to one another fixed morphological relationships, it would certainly have been an easy matter for such a power to have given to the larvæ of butterflies some small character which would have distinguished them as such, and which would in some measure have impressed them with the stamp of "*Rhopalocera*." Of such a character we find no trace however; on the contrary, everything goes to show that the transformations of the organic world result entirely from external influences.

### III.

#### INCONGRUENCES IN OTHER ORDERS OF INSECTS.

ALTHOUGH the order Lepidoptera is for many reasons especially favourable for an investigation such as that undertaken in the previous section, it will nevertheless be advantageous to inquire into the form-relationships of the two chief stages in some other orders of metamorphic insects, and to investigate whether in these cases the formation of systematic groups also coincides with common conditions of life.

#### HYMENOPTERA.

In this order there cannot be the least doubt as to the form-relationship of the imagines. The characteristic combination of the pro- and mesothorax, the number and venation of the wings, and the mouth-organs formed for biting and licking, are found throughout the whole order, and leave no doubt that the Hymenoptera are well based on their imaginal characters.

But it is quite different with the larvæ. It may be boldly asserted that the order would never have been founded if the larvæ only had been

known. Two distinct larval types here occur, the one—caterpillar-like—possessing a distinct horny head provided with the typical masticatory organs of insects, and a body having thirteen segments, to which, in addition to a variable number of abdominal legs, there are always attached three pairs of horny thoracic legs : the other type is maggot-shaped, without the horny head, and is entirely destitute of mouth-organs, or at least of the three pairs of typical insect jaws, and is also without abdominal and thoracic legs. The number of segments is extremely variable ; the larvæ of the saw-flies have thirteen besides the head, the maggot-shaped larvæ of bees possess fourteen segments altogether, and the gall-flies and ichneumons only twelve or ten. We should be much mistaken also if we expected to find connecting characters in the internal organs. The intestine is quite different in the two types of larvæ, the posterior opening being absent in the maggot-like grubs ; at most only the tracheal and nervous systems show a certain agreement, but this is not complete.

The order Hymenoptera, precisely speaking and conceived only morphologically, exists therefore but in the imagines ; in the larvæ there exist only the caterpillar- and maggot-formed groups. The former shows a great resemblance to Lepidopterous larvæ, and in the absence of all knowledge of the further development it might be attempted to



unite them with these into one group. The two certainly differ in certain details of structure in the mouth-organs and in the number of segments, abdominal legs, &c., to a sufficient extent to warrant their being considered as two sub-orders of one larval order; but they would in any case be regarded as much more nearly related in form than the caterpillar- and maggot-like types of the Hymenopterous larvæ.

Is it not conceivable, however, that the imagines of the Hymenoptera—that ichneumons and wasps may be only accidentally alike, and that they have in fact arisen from quite distinct ancestral forms, the one having proceeded with the Lepidopterous caterpillars from one root, and the other with the grub-like Dipterous larvæ from another root?

This is certainly not the case; the common characters are too deep-seated to allow the supposition that the resemblance is here only superficial. From the structure of the imagines alone the common origin of all the Hymenoptera may be inferred with great probability. This would be raised into a certainty if we could demonstrate the phyletic development of the maggot-formed out of the caterpillar-formed Hymenopterous larvæ by means of the ontogeny of the former. From the beautiful investigations of Bütschli on the embryonic development of bees<sup>1</sup> we know that the

<sup>1</sup> Zeitschrift für wissenschaftl. Zoologie, vol. xx. p. 519.

embryo of the grub possesses a complete head, consisting of four segments and provided with the three typical pairs of jaws. These head segments do not subsequently become formed into a true horny head, but shrivel up; whilst the jaws disappear with the exception of the first pair, which are retained in the form of soft processes with small horny points. We know also that from the three foremost segments of the embryo the three typical pairs of legs are developed in the form of round buds, just as they first appear in all insects.<sup>2</sup> These rudimentary limbs undergo complete degeneration before the birth of the larva, as also do those of the whole<sup>3</sup> of the remaining segments, which, even in this primitive condition, show a small difference to the three foremost rudimentary legs.

The grub-like larvæ of the Hymenoptera have therefore descended from forms which possessed a horny head with antennæ and three pairs of gnathites and a 13-segmented body, of which the three foremost segments were provided with legs

<sup>2</sup> [See for instance Lubbock's "Origin and Metamorphoses of Insects," chap. iii.; and F. M. Balfour's "Comparative Embryology," vol. i., 1880, pp. 327—356. This last work contains an admirable *résumé* of our knowledge of the embryonic development of insects up to the date of publication. R.M.]

<sup>3</sup> Are not the 4th, 11th, and 12th segments destitute of the rudiments of legs as in the larvæ of all existing saw-flies? I might almost infer this from Bütschli's figures (see for instance Pl. XXV., Fig. 17A).

differing somewhat from those of the other segments; that is to say, they have descended from larvæ which possessed a structure generally similar to that of the existing saw-fly larvæ. The common derivation of all the Hymenoptera from one source is thus established with certainty.<sup>4</sup>

But upon what does this great inequality in the form-relationship of the larvæ and imagines depend? The existing maggot-like grubs are without doubt much further removed from the active caterpillar-like larvæ than are the saw-flies from the Aculeate Hymenoptera. Whilst these two groups differ only through various modifications of the typical parts (limbs, &c.), their larvæ are separable by much deeper-seated distinctions;

<sup>4</sup> [The grub-formed Hymenopterous larvæ, like the larvæ of all other holometabolous insects, thus represent an acquired degenerative stage in the development, *i.e.* an adaptation to the conditions of life at that stage. Bearing in mind the above-quoted observations of Bütschli and the caterpillar-like form of the Terebrantiate group of Hymenopterous larvæ, the following remarks of Balfour's (*loc. cit.* p. 353), appear highly suggestive:—"While in a general way it is clear that the larval forms of insects cannot be expected to throw much light on the nature of insect ancestors, it does nevertheless appear to me probable that such forms as the caterpillars of the Lepidoptera are not without a meaning in this respect. It is easy to conceive that even a secondary larval form may have been produced by the prolongation of one of the embryonic stages; and the general similarity of a caterpillar to *Peripatus*, and the retention by it of post-thoracic appendages, are facts which appear to favour this view of the origin of the caterpillar form." See also Sir John Lubbock, *loc. cit.*, pp. 93 and 95. R.M.]

limbs of typical importance entirely vanish in the one group, but in the other attain to complete development.

In the Hymenoptera there exists therefore a very considerable incongruence in the systems based morphologically, *i. e.* on the pure form-relationships of the larvæ and of the imagines. The reason of this is not difficult to find: *the conditions of life differ much less in the case of the imagines than in that of the larvæ.* In the former the conditions of life are similar in their broad features. Hymenoptera live chiefly in the air and fly by day, and in their mode of obtaining food do not present any considerable differences. Their larvæ, on the other hand, live under almost diametrically opposite conditions. Those of the saw-flies live after the manner of caterpillars upon or in plants, in both cases their peculiar locomotion being adapted for the acquisition and their masticatory organs for the reduction of food. The larvæ of the other Hymenoptera, however, do not as a rule require any means of locomotion for reaching nor any organs of mastication for swallowing their food, since they are fed in cells, like the bees and wasps, or grow up in plant galls of which they suck the juice, or are parasitic on other insects by whose blood they are nourished. We can readily comprehend that in the whole of this last group the legs should disappear, that the jaws should likewise vanish or should become



diminished to one pair retained in a much reduced condition, that the horny casing of the head, the surface of attachment of the muscles of the jaws, should consequently be lost, and that even the segments of the head itself should become more or less shrivelled up as the organs of sense therein located became suppressed.

The incongruence manifests itself however in yet another manner than by the relatively greater morphological divergence of the larvæ: a different grouping is possible for the larvæ and for the imagines. If we divide the Hymenoptera simply according to the form-relationships of the imagines, the old division into the two sub-orders *Terebrantia* or *Ditrocha* and *Aculeata* or *Mono-trocha* will be the most correct. The distinguishing characters of a sting or ovipositor and a one- or two-jointed trochanter are still of the greatest value. But these two sub-orders do not by any means correspond with the two types of larvæ since, in the *Terebrantia*, there occur families with both caterpillar-formed and maggot-formed larvæ.

The cause is to be found in that a portion of these families possess larvæ which are parasitic in other insects or in galls, their bodily structure having by these means become transformed in a quite different direction. The mode of life of the imagines is, on the other hand, essentially the same.

We have here therefore another case like that which we met with among the Rhopalocerous Lepidoptera, in which the imagines appear to be capable of being formed into a higher group than the larvæ, because the former live under conditions of life which are on the whole similar whilst the latter live under very divergent conditions.

The old division of the Hymenoptera into two sub-orders has certainly been abandoned in the later zoological text-books; they are now divided into three:—saw-flies, parasitic, and aculeate Hymenoptera; but even this arrangement has been adopted with reference to the different structure of the larvæ. Whether this system is better than the older, *i.e.* whether it better expresses the *genealogical* relationship, I will not now stop to investigate.<sup>5</sup>

#### DIPTERA.

The imagines of the Diptera (*genuina*), with the exception of the *Aphaniptera* and *Pupipara*, agree in all their chief characters, such as the number

<sup>5</sup> [In the most recent works dealing with this order six groups, based on the character of the imagines are recognized, viz.:—*Tubulifera*, *Terebrantia*, *Pupivora*, *Heterogyna Fossores*, and *Melilifera*. (See, for instance, F. P. Pascoe's "Zoological Classification," 2nd ed. p. 147.) Of these groups the larvæ of the *Terebrantia* as thus restricted are all of the caterpillar type (*Tenthredinidæ* and *Siricidæ*), whilst those of the other groups are maggot-shaped. For a description of the development of the remarkable aberrant larva of *Platygaster*, see Ganin in Zeit. f. wissenschaftl. Zool., vol. xix. 1869. R.M.]

and structure of the wings, the number and joints of the legs, the peculiar formation of the thorax (fusion of the three segments) ;<sup>6</sup> and even the structure of the mouth organs varies only within narrow limits. This is in accordance with their mode of life, which is very uniform in its main features : all the true Diptera live in the light, moving chiefly by means of flight, but having also the power of running ; all those which take food in the imago condition feed upon fluids. Their larvæ, on the other hand, are formed on two essentially different types, the one—which I shall designate as the gnat-type—possessing a horny head with eyes, three pairs of jaws, and long or short antennæ, together with a 12- or 13-segmented body, which is never provided with the three typical pairs of thoracic legs, but frequently has the so-called abdominal legs on the first and last segments. The other Dipterous larvæ are maggot-shaped and without a horny head, or in fact without any head, since the first segment, the homologue of the head, can in no case be distinguished through its being larger than the others ; it is on the contrary much smaller. The typical insect mouth-parts are entirely absent, being replaced by a variously formed and quite peculiar arrangement of hooks situated on the mouth and capable of protrusion.

\* [For recent investigations on the structure of the thorax in Diptera, see a paper by Mr. A. Hammond, in Journ. Linn. Soc., Zoology, vol xv. p. 9. R.M.]

Never more than eleven segments are present besides the first, which is destitute of eyes ; neither are abdominal legs ever developed.

The mode of life differs very considerably in the two groups of larvæ. Although the Dipterous maggots are not as a rule quite incapable of locomotion like the grubs of the Hymenoptera (bees, ichneumons), the majority are nevertheless possessed of but little power of movement in the food-substance on which they were deposited as eggs. They do not go in search of food, either because they are parasitic in other insects in the same manner as the ichneumons (*Tachina*), or else they live on decaying animal or vegetable substances or amidst large swarms of their prey, like the larvæ of the *Syrphidæ* amongst *Aphides*. They generally undergo pupation in the same place as that which they inhabit as larvæ and indeed in their larval skin which hardens into an oval pupa-case. Some few leave their feeding place and pupate after traversing a short distance (*Eristalis*).

As in the case of the Hymenoptera the structure of the larvæ can here also be explained by peculiarities in their mode of life. Creatures which live in a mass of food neither require special organs of locomotion nor specially developed organs of sense (eyes). They have no use for the three pairs of jaws since they only feed on liquid substances, and the hooks within the mouth



do not serve for the reduction of food but only for fastening the whole body. With the jaws and their muscular system there likewise disappears the necessity for a hard surface of attachment, *i.e.* a corneous head.

The mode of life of the larvæ of the gnat-type is quite different in most points. The majority, and indeed the most typically formed of these, have to go in search of their food, whether they are predaceous, such as the *Culicidæ* and many of the other *Nemocera* (*Corethra*, *Simulium*), or whether they feed on plants, which they in some cases weave into a protective dwelling tube (certain species of *Chironomus*). Many live in water and move with great rapidity; others bury in the earth or in vegetable substances; and even those species which live on fungi sometimes wander great distances, as in the well-known case of the "army worm" where thousands of the larvæ of *Sciara Thomæ* thus migrate.

Now the two types of larvæ correspond generally with the two large groups into which, as it appears to me correctly, the *Diptera* (*genuina*) are as a rule divided. In this respect there is therefore an equality of form-relationship—the grouping is the same, and the incongruence depends only upon the form-divergence between the two kinds of larvæ being greater than between the two kinds of imagines.<sup>7</sup>

<sup>7</sup> I am familiar with the fact that the two sub-orders of

That the form-divergence is greater in the larvæ than in the imagines cannot be doubted; that this distant form-relationship cannot, however, be referred to a very remote common origin, *i. e.* to a very remote blood-relationship, not only appears from the existence of transition-forms between the two sub-orders, but can be demonstrated here, as in the case of the Hymenoptera, by the embryonic development of the maggot-like larvæ.

Seventeen years ago I showed<sup>8</sup> that the grub-formed larvæ of the *Muscidæ* in the embryonic state possessed a well-developed head with antennæ and three pairs of jaws, but that later in the course of the embryonic development a marked reduc-

true Diptera, the short-horned (*Brachycera*), and the long-horned (*Nemocera*), are not sharply limited; and I am likewise well acquainted with the circumstance that there are forms which connect the two larval types. The connecting forms of the imagines do not, however, always coincide with the intermediate larval forms, so that there here arises a second and very striking incongruence of morphological relationship which depends only upon the circumstance that the one stage has diverged in form more widely than the other through a greater divergence in the conditions of life. The difficulty is in these cases aggravated because an apparent is added to the true form-relationship through convergence, so that without going into exact details the form and genealogical relationships of the Diptera cannot be distinguished. It would be of great interest for other reasons to make this investigation, and I hope to be able to find leisure for this purpose at some future period.

<sup>8</sup> "Entwicklung der Dipteren." Leipzig, 1864.

tion and transformation of these parts takes place, so that finally the four head segments appear as a single small ring formed from the coalesced pairs of maxillæ, whilst the so-called "fore-head" (the first head segment), together with the mandibles, becomes transformed into a suctorial-head armed with hooks and lying within the body. At the time of writing I drew no conclusion from these facts with reference to the phyletic development of these larval forms; nor did Bütschli, six years later, in the precisely analogous case of the larvæ of the bees. The inference is, however, so obvious that it is astonishing that it should not have been drawn till the present time.<sup>9</sup>

There can be no doubt that the maggot-like larvæ of insects are not by any means ancient forms, but are, on the contrary, quite recent, as first pointed out by Fritz Müller,<sup>10</sup> and afterwards by Packard<sup>11</sup> and Brauer,<sup>12</sup> and as is maintained in the latest work by Paul Mayer<sup>13</sup> on the phylogeny of insects.

<sup>9</sup> Lubbock concludes from the presence of thoracic legs in the embryonic larva of bees that these have been derived from a larva of the *Campodea* type, but he overlooks the fact that the rudiments of the abdominal legs are also present; *loc. cit.*, p. 28.

<sup>10</sup> "Für Darwin," Leipzig, 1864, p. 8.

<sup>11</sup> Mem. Peabody Acad. of Science, vol. i. No. 3.

<sup>12</sup> Verhandl. Wien. Zoolog. Botan. Gesellsch. 1869, p. 310.

<sup>13</sup> Über Ontogenie und Phylogenie der Insekten. Eine akademische Preisschrift. Jen. Zeitschrift. Bd. x. Neue Folge,

The Dipterous maggots have evidently descended from which a larval form possessed a horny head with antennæ and three pairs of jaws, but which had no appendages to the abdominal segments; they are therefore ordinary Dipterous larvæ of the gnat-type which have become modified in a quite peculiar manner and adapted to a new mode of life, just as the grubs of the Hymenoptera are larvæ of the saw-fly type, which have become similarly transformed, although by no means in the same manner. The resemblance between the two types of larva is to a great extent purely external, and depends upon the

iii. Heft 2. 1876. [Some remarks by F. M. Balfour on the origin of certain larval forms have already been quoted in a previous note (p. 485). This author further states:—"The fact that in a majority of instances it is possible to trace an intimate connection between the surroundings of a larva and its organization proves in the clearest way *that the characters of the majority of existing larval forms of insects have owed their origin to secondary adaptations.* A few instances will illustrate this point:—In the simplest types of metamorphosis, *e.g.* those of the Orthoptera genuina, the larva has precisely the same habits as the adult. We find that a caterpillar form is assumed by phytophagous larvæ amongst the Lepidoptera, Hymenoptera, and Coleoptera. Where the larva has not to go in search of its nutriment the grub-like apodous form is assumed. The existence of such an apodous larva is especially striking in the Hymenoptera, in that rudiments of thoracic and abdominal appendages are present in the embryo and disappear again in the larva. . . . It follows from the above that the development of such forms as the Orthoptera genuina is more primitive than that of the holometabolous forms, &c." Comparative Embryology, vol. 1, p. 352. R.M.]



process designated "convergence" by Oscar Schmidt, *i. e.* upon the adaptation of heterogeneous animal forms to similar conditions of life. By adaptation to a life within 'a mass of fluid nutriment, the caterpillar-formed larvæ of the Hymenoptera and the *Tipula*-like larvæ of the Diptera have acquired a similar external appearance, and many similarities in internal structure, or, in brief, have attained to a considerable degree of form-relationship, which would certainly have tended to conceal the wide divergence in blood-relationship did not the embryological forms on the one side and the imagines on the other provide us with an explanation.

It is certainly of great interest that in another order of insects—the Coleoptera—grub-formed larvæ occur quite irregularly, and their origin can be here traced to precisely the same conditions of life as those which have produced the grubs of bees. I refer to the honey-devouring larvæ of the *Meloïdæ* (*Meloë*, *Sitaris*, *Cantharis*). The case is the more instructive, inasmuch that the six-legged larval form is not yet relegated to the development within the egg, but is retained in the first larval stage. In the *second larval stage* the maggot-form is first assumed, although this is certainly not so well pronounced as in the Diptera or Hymenoptera, as neither the head nor the thoracic legs are so completely suppressed as in these orders. Nevertheless, these parts have

made a great advance in the process of transformation.

The grub-like larvæ of the Hymenoptera and Diptera appear to me especially instructive with reference to the main question of the causes of transformation. The reply to the questions: what gives the impetus to change? is this impetus internal or external? can scarcely be given with greater clearness than here. If these larvæ have abandoned their ancestral form and have acquired a widely divergent structure, arising not only from suppression but partly also from an essentially new differentiation (suctorial head of the *Muscidæ*), and if these structural changes show a close adaptation to the existing conditions of life, from these considerations alone it is difficult to conceive how such transformations can depend upon the action of a phyletic force. The latter must have foreseen that at precisely this or that fixed period of time the ancestors of these larvæ would have been placed under conditions of life which would make it desirable for them to be modified into the maggot-type. But if at the same time the imagines are removed in a less degree from those of the caterpillar-like larvæ, this divergence being in exact relation with the deviations in the conditions of life, I at least fail to see how we can escape the consequence that it is the external conditions of life which produce the transformations and induce the organism to

change. It is to me incomprehensible how one and the same vital force can in the same individual induce one stage to become transformed feebly and the other stage strongly, these transformations corresponding in extent with the stronger or weaker deviations in the conditions of life to which the organism is exposed in the two stages; to say nothing of the fact that by such unequal divergences the idea of a perfect system (creative thought) is completely upset.

Nor can the objection be raised that we are here only concerned with insignificant changes—with nothing more than the arrested development of single organs and so forth, in brief, only with those changes which can be ascribed to the action of the environment.

We are here as little concerned with a mere suppression of organs through arrested development as in the case of the Cirripedia; the transformation and reconstruction of the whole body goes even much further than in these Crustacea, although not so conspicuous externally. Where do we elsewhere find insects having the head inside a cavity of the body (sectorial head of the *Muscidæ*), and of which the foremost segment—the physiological representative of the head—consists entirely of the coalesced antennæ and pairs of maxillæ?

The incongruences in the form-relationships are, however, exceedingly numerous in the case

of the Diptera, and a special treatise would be necessary to discuss them thoroughly. I may here mention only one case, because the inequality shows itself in this instance in a quite opposite sense.

Gerstäcker, who is certainly a competent entomologist, divides the Diptera into three tribes, viz. the *Diptera genuina*, the *Pupipara*, and the *Aphaniptera*. The latter, the fleas, possess in their divided thoracic segments and in their jointed labial appendages characters so widely divergent from those of the true Diptera and of the *Pupipara* that Latreille and the English zoologists have separated them entirely from the Diptera and have raised them into a separate order.<sup>14</sup> Those who do not agree in this arrangement, but with Gerstäcker include the fleas under the Diptera, will nevertheless admit that the morphological divergence between the *Aphaniptera* and the two other tribes is far greater than that which exists between the latter. Now the larvæ of the fleas are completely similar in structure to those of the gnat-type, since they possess a corneous head with the typical mouth parts and antennæ and a 13-segmented body devoid of legs. Were we only acquainted with the larvæ of the fleas we should

<sup>14</sup> [The *Aphaniptera* are now recognized in this country as a sub-order of Diptera. See, for instance, Huxley's "Anatomy of Invertebrated Animals," p. 425, and Pascoe's "Zoological Classification," 2nd ed. p. 122. R.M.]



rank them with the true Diptera under the sub-order *Nemocera*. On first finding such a larva we should expect to see emerge from the pupa a small gnat.

While the imagines of the *Nemocera* and *Aphaniptera* thus show but a very remote form-relationship their larvæ are very closely allied. Can any one doubt that in this case it is not the larva but the imago which has diverged to the greatest extent? Have not the fleas moreover become adapted to conditions of life widely different from those of all other Diptera, whilst their larvæ do not differ in this respect from many other Dipterous larvæ?

We have here, therefore, another case of unequal phyletic development, which manifests itself in the entirely different form-relationship of the larvæ and the imagines. Thus in this case, as in that of the Lepidoptera, it is sometimes the larval and at other times the imaginal stage which has experienced the greatest transformation, and, as in the order mentioned, the objection that a phyletic vital force produces greater and more important differentiations in the higher imaginal stage than in the lower or less developed larval stage, is equally ineffectual.

If, however, it be asked whether the unequal phyletic development depends in this case upon an unequal number of transforming impulses which the two stages may have experienced during an

equal period of time, this must be decidedly answered in the negative. The unequal development obviously depends in this case, as in the higher systematic groups of the Lepidoptera, upon the unequal value of the parts affected by the changes. These parts are on the one side of small importance, and on the other side of great importance, to the whole structure of the insect. This is shown in the last-mentioned case of the fleas, where, of the typical parts of the body, only the wings have become rudimentary, whilst the antennæ, mouth-parts, and legs, and even the form and mode of segmentation (free thoracic segments), must have suffered most important modifications; their larvæ, on the other hand, can have experienced only unimportant changes, since they still agree in all typical parts with those of the gnat-type.

Although therefore in this and in similar cases a greater number of transforming impulses may well have occurred on the one side than on the other—and it is indeed highly probable that this number has not been absolutely the same—nevertheless the chief cause of the striking incongruence is not to be found therein, but rather in the *strength* of the transforming impulses, if I may be permitted to employ this figure, or, more precisely expressed, in the importance of the parts which become changed and at the same time in the amount of change.

In this conclusion there is implied as it appears to me an important theoretical result which tells further against the efficacy of a phyletic force.

If the so-called "typical parts" of an animal disappear completely through the action of the environment only, and still further, if these parts can become so entirely modified as to give rise to quite new and again typical structures (suctorial head of the *Muscidae*) without the typical parts of the other stage of the same individual being thereby modified and transformed into a new type of structure, how can we maintain a distinction between typical and non-typical parts with respect to their origin? But if a difference exists with respect only to the physiological importance of such parts, *i.e.* their importance for the equilibrium of the whole organization, while, with reference to transformation and suppression, exactly the same influences appear to be effective as those which bring about a change in or a disappearance of the so-called adventitious parts, where is there left any scope for the operation of the supposed phyletic force? What right have we to assume that the typical structures arise by the action of a vital force? Nevertheless this is the final refuge of those who are bound to admit that a great number of parts or characters of an animal can become changed, suppressed, or even produced by the action of the environment.

## IV.

## SUMMARY AND CONCLUSION.

THE question heading the second section of this essay must at the conclusion of the investigation be answered in the negative. The form-relationship of the larvæ does not always coincide with that of the imagines, or, in other words, a system based entirely on the morphology of the larvæ does not always coincide with that founded entirely on the morphology of the imagines.

Two kinds of incongruence here present themselves. The first arises from the different amount of divergence between two systematic groups in the larvæ and in the imagines, these groups being of equal extent. The second form of incongruence consists essentially in that the two stages form systematic groups of different extents, either the one stage constituting a group of a higher order than the other and therefore forming a group of unequal value, or else the two stages form groups of equal systematic value, these groups, however, not coinciding in extent, but the one overlapping the other.

This second form of incongruence is very



frequently connected with the first kind, and is mostly the direct consequence of the latter.

The cause of the incongruences is to be found in unequal phyletic development, either the one stage within the same period of time having been influenced by a greater number of transforming-impulses than the other, or else these impulses have been different in strength, *i.e.* have affected parts of greater or less physiological value, or have influenced parts of equal value with unequal strength.

In all these cases in which there are deep-rooted form-differences, it can be shown that these correspond exactly with inequalities in the conditions of life, this correspondence being in two directions, viz. in strength and in extent: the former determines the *degree* of form-difference, the latter its *extent* throughout a larger or smaller group of species.

The different forms of incongruence are manifested in the following manner:—

(1.) Different amount of form-divergence between the larvæ on the one side and the imagines on the other. Among the Lepidoptera this is found most frequently in varieties and species, and there is evidence to show that in this case the one stage has been affected by transforming influences, either alone (varieties), or at any rate to a greater extent (species). In the last case it can be shown in many ways that one

stage (the larva) has actually remained at an older phyletic grade (*Deilebhila* species). Incongruences of this kind depending entirely upon the more frequent action of transforming impulses can only become observable in the smaller systematic groups, in the larger they elude comparative examination. In the higher groups unequal form-divergence may be produced by the transforming impulses affecting parts of unequal physiological and morphological value, or by their influencing parts of equal value in different degrees. All effects of this kind can, however, only become manifest after a long-continued accumulation of single changes, *i. e.* only in those systematic groups which require a long period of time for their formation. By this means we can completely explain why the incongruences of form-divergence continually diminish from varieties to genera, and then increase again from genera upwards through families, tribes, and sub-orders : the first diminishing incongruence depends upon an *unequal number* of transforming impulses, the latter increasing incongruence depends upon the *unequal power* of these impulses.

Cases of the second kind are found among the Lepidopterous families, and especially in the higher groups (*Rhopalocera* and *Heterocera*), and appear still more striking in the higher groups of the Hymenoptera and Diptera. Thus the caterpillar shaped and maggot-formed larvæ of the

Hymenoptera differ from one another to a much greater extent than their imagines, since the latter have experienced a complete transformation of typical parts; whilst in the caterpillar-formed larvæ these parts vary only within moderate limits. Similarly in the case of the Diptera, of which the gnat-like larvæ diverge more widely from those of the grub type than do the gnats from the true flies. On the other hand the divergence between the imagines of the fleas and gnats is considerably greater than that between their larvæ—indeed the larvæ of the fleas would have to be ranked as a family of the sub-order of the gnat-like larvæ if we wished to carry out a larval classification. By this it is also made evident that these unequal divergences, when they occur in the higher systematic groups, always induce at the same time the second form of incongruence—that of the formation of unequal systematic groups.

In general whenever such unequal divergences occur in the higher groups they run parallel with a strong deviation in the conditions of life. If these differ more strongly on the side of the larvæ, we find that the structure of the latter likewise diverges the more widely, and that their form-relationship is in consequence made more remote (saw-flies and ichneumons, gnats and flies); if, on the other hand, the difference in the conditions of life is greater on the side of the imagines, we find among the latter the greater

morphological divergence (butterflies and moths, gnats and fleas).

(2.) The second chief form of incongruence consists in the formation of different systematic groups by the larvæ and the imagines, if the latter are grouped simply according to their form-relationship without reference to their genetic affinities. This incongruence again shows itself in two forms—in the formation of groups of unequal value, and the formation of groups equal in value but unequal in extent, *i. e.* of overlapping instead of coinciding groups.

Of these two forms the first arises as the direct result of a different amount of divergence. Thus the larvæ of the fleas, on account of their small divergence from those of the gnats,<sup>2</sup> could only lay claim to the rank of a *family*, whilst their imagines are separated from the gnats by such a wide form-divergence that they are correctly ranked as a distinct *tribe* or *sub-order*.

The inequalities in the lowest groups, varieties, can be regarded in a precisely similar manner. If the larva of a species has become split up into two local forms, but not the imago, each of the two larval forms possesses only the rank of a *variety*, whilst the imaginal form has the value of a *species*.

Less simple are the causes of the phenomenon that in the one stage the lower groups can be combined into one of higher rank, whilst the other



stage does not attain to this high rank. Such a condition appears especially complicated when the two stages can again be formed into groups of a still higher rank.

This is the case in the tribe *Rhopalocera*, which is founded on the imagines alone, the larvæ forming only families of butterflies. Both stages can however be again combined into the highest systematic group of the Lepidoptera.

In this case also the difference in the value of the systematic groups formed by the two stages corresponds precisely with the difference in the conditions of life. This appears very distinctly when there are several sub-groups on each side, and not when, as in the fleas, only one family is present as a tribe on the one side and on the other as a family. Thus in the butterflies, on the one side there are numerous families combined into the higher rank of a sub-order (imagines), whilst on the other side (larvæ) a group of the same extent cannot be formed. In this instance it can be distinctly shown that the combination of the families into a group of a higher order, as is possible on the side of the imagines, corresponds exactly with the limits in which the conditions of life deviate from those of other Lepidopterous families. The group of butterflies corresponds with an equally large circle of uniform conditions of life, whilst a similar uniformity is wanting on the side of the larvæ.

The second kind of unequal group formation arises from the circumstance that groups of equal value can be formed from the two stages, but these groups do not possess the same limits—they overlap, and only coincide in part.

This is most clearly seen in the order Hymenoptera, in which both larvæ and imagines form two well-defined morphological sub-orders, but in such a manner that the one larval form not only prevails throughout the whole of the one sub-order of the imagines, but also extends beyond and spreads over a great portion of the other imaginal sub-order.

Here again the dependence of this phenomenon upon the influence of the environment is very distinct, since it can be demonstrated (by the embryology of bees) that the one form of larva—the maggot-type—although the structure now diverges so widely, has been developed from the other form, and that it must have arisen by adaptation to certain widely divergent conditions of life.

This form of incongruence is always connected with unequal divergence between the two stages of the one systematic group—in this case the *Terebrantia*. The larvæ of this imaginal group partly possess caterpillar-like (*Phytosphæces*) and partly maggot-formed (*Entomosphæces*) larvæ, and differ from one another to a considerably greater extent than the saw-flies from the ichneumons.<sup>1</sup> The

<sup>1</sup> [This illustration of course only applies to the old arrange-

final cause of the incongruence lies therefore in this case also in the fact that one stage has suffered stronger changes than the other, so that a deeper division of the group has occurred in the former than in the latter.

The analogous incongruences in single families of the Lepidoptera may have arisen in a similar manner, as has already been more clearly shown above; only in these cases we are as yet unable to prove in detail that the larval structure has become more strongly changed through special external conditions of life than that of the imagines.

In the smallest systematic group—varieties, it has been possible to furnish some proof of this. The one-sided change here depends in part upon the *direct action* of external influences (seasonal dimorphism, climatic variation), and it can be shown that these influences (temperature) acted only on the one stage, and accordingly induced change in this alone whilst the other stage remained unaltered.

It has now been shown—not indeed in every individual case, but for each of the different kinds of incongruence of form-relationship—that there is an exact parallelism corresponding throughout with the incongruence in the conditions of life. Wherever the forms diverge more widely in one

ment of the Hymenoptera into *Terebrantia* and *Aculeata*. See also note 5, p. 488. R.M.]

stage than in the other we also find more widely divergent conditions of life; wherever the morphological systemy of one stage fails to coincide with that of the other—whether in the extent or in the value of the groups—the conditions of life in that stage also diverge, either more widely or at the same time within other limits; whenever a morphological group can be constructed from one stage but not from the other, we find that this stage alone is submitted to certain common conditions of life which fail in the other stage.

The law that the divergence in form always corresponds exactly with the divergence in the conditions of life<sup>2</sup> has accordingly received confirmation in all cases where we have been able to pronounce judgment. Unequal form-divergences correspond precisely with unequal divergence in the conditions of life, and community of form appears within exactly the same limits as community in the conditions of life.

These investigations may thus be concluded with the following law:—In types of similar origin, *i.e.* having the same blood-relationship, the degree of morphological relationship corresponds exactly

\* [Eng. ed. This law is perhaps a little too restricted, inasmuch as it is theoretically conceivable that the organism may be able to adapt itself to similar conditions of life in different ways; differences of form could thus depend sometimes upon differences of adaptation and not upon differences in the conditions of life, or, as I have formerly expressed it, it is not necessary to allow always only *one* best mode of adaptation.]



with the degree of difference in the conditions of life in the two stages.

With respect to the question as to the final cause of transformation this result is certainly of the greatest importance.

The interdependence of structure and function has often been insisted upon, but so long as this has reference only to the agreement of each particular form with some special mode of life, this harmony could still be regarded as the result of a directive power ; but when in metamorphic forms we not only see a double agreement between structure and function, but also that the transformation of the form occurs in the two chief developmental stages in successive steps at unequal rates and with unequal strength and rhythm, we must—at least so it appears to me—abandon the idea of an inherent transforming force ; and this becomes the more necessary when, by means of the opposite and extremely simple assumption that transformations result entirely from the response of the organism to the actions of the environment, all the phenomena—so far as our knowledge of facts at present extends—can be satisfactorily explained. A power compelling transformation, *i.e.* a phyletic vital force, must be abandoned, on the double ground that it is incapable of explaining the phenomena (incongruence and unequal phyletic development), and further because it is superfluous.

Against the latter half of this argument there can at most be raised but the one objection that the phenomena of transformation are not completely represented by the cases here analysed. In so far as this signifies that the whole organic world, animal and vegetable, has not been comprised within the investigation this objection is quite valid. The question may be raised as to the limit to which we may venture to extend the results obtained from one small group of forms. I shall return to this question in the last essay.

But if by this objection it is meant that the restricted field of the investigation enables us to actually analyse only a portion of the occurring transformations,<sup>3</sup> and indeed only those cases, the dependence of which upon the external conditions of life would be generally admitted, I will not let pass the opportunity of once more pointing out at the conclusion of the present essay that the incongruences shown to exist by no means depend only upon those more superficial characters the remodelling of which in accordance with the external conditions of life may be most easily discerned and is most difficult to deny, but that in certain cases (maggot-like Dipterous larvæ) it is

<sup>3</sup> [It must be understood that the word rendered here and elsewhere throughout this work as "transformation" is not to be taken in the narrow sense of metamorphosis, but as having the much broader meaning of a change of any kind incurred by an organism. Metamorphosis is in fact but one phase of transformation. R.M.]

precisely the "typical" parts which become partly suppressed and partly converted into an entirely new structure. From the ancient typical appendages there have here arisen new structures, which again have every right to be considered as typical. This transformation is not to be compared with that experienced by the swimming appendages of the *Nauplius*-like ancestor of an *Apus* or *Branchipus* which have become mandibulate, nor with the transformation which the anterior limbs must have gone through in the reptilian ancestors of birds. The changes in question (Dipterous larvæ) go still further and are more profound. I lay great emphasis upon this because we have here one of the few cases which show that typical parts are quite as dependent upon the environment as untypical structures, and that the former are not only able to become adapted to external conditions by small modifications—as shown in a most striking manner by the transformations of the appendages in the Crustacea and Vertebrata—but that these parts can become modelled on an entirely new type which, when perfected, gives no means of divining its mode of origin. I may here repeat a former statement:—With reference to the causes of their origination we have no grounds for drawing a distinction between typical and untypical structures.

It may be mentioned in concluding that quite analogous although less sharply defined results are

arrived at if, instead of fixing our attention upon the different stages of a systematic group in their phyletic development, we only compare the different functional parts (organs in the wide sense) of the organisms.

A complete parallel can be drawn between the two classes of developmental phenomena. From the very different systematic values attached by taxonomists to this or that organ in a group of animals, it may be concluded that the individual parts of an organism are to a certain extent independent, and that each can vary independently, when affected either entirely alone or in a preponderating degree by transforming impulses, without all the other parts of the organism likewise suffering transformation, or at least without their becoming modified in an equal degree. Did all the parts and organs in two groups of animals diverge from each other to the same extent, the systematic value of such parts would be perfectly equal; we should, for example, be able to distinguish and characterize two genera of the family of mice by their kidneys, their liver, their salivary glands, or by the histological structure of their hair or muscles, or even by differences in their myology, &c. equally as well as by their teeth, length of toes, &c. It is true that such a diagnosis has yet to be attempted; but it may safely be predicted that it would not succeed. Judging from all the facts at present before us, the individual parts—and



- especially those connected in their physiological action, *i.e.* the system of organs—do not keep pace with reference to the modifications which the species undergoes in the course of time ; at one period one system and at another period some other system of organs advances while the others remain behind.

This corresponds exactly with the result already deduced from the unparallel development of the independent ontogenetic stages. If the inequality in the phyletic development is more sharply pronounced in this than in the last class of cases, this can be explained by the greater degree of correlation which exists between the individual systems of organs in any single organism as compared with that existing between the ontogenetic stages, which, although developed from one another, are nevertheless almost completely independent. We should have expected *à priori* that a strong correlation would have here existed, but as a matter of fact this is not the case, or is so only in a very small degree.

Just as in the stages of metamorphosis the inequality of phyletic development becomes the more obliterated the more distant and comprehensive, or, in other words, the greater the period of existence of the groups which we compare, so does the unequal divergence of the systems of organs become obliterated as we bring into comparison larger and larger systematic groups.

It is not inconceivable—although a clear proof of this is certainly as yet wanting—that a variety of the ancestral species would differ only in one single character, such as hairiness, colour, or marking, and such instances would thus agree precisely with the foregoing cases in which only the caterpillar or the butterfly formed a variety. All the more profound modifications however—such for instance as those which determine the difference between two species—are never limited to one character, but always affect several, this being explicable by correlation, which, as Darwin has shown in the case of dogs, may cause modifications in the skull of those breeds having hanging ears in consequence of this last character alone. It must be admitted however that one organ only would be originally affected by a modifying influence. Thus, I am acquainted with two species of a genus of Daphniacea which are so closely allied that they can only be distinguished from one another by a close comparison of individual details. But whilst most of the external and internal organs are almost identical in the two species the sperm-cells of the males differ in a most striking manner, in one species resembling an Australian boomerang in form and in the other being spherical! An analogous instance is furnished by *Daphnia Pulex* and *D. Magna*, two species which were for a long time confounded. Nearly all the parts of the body are here exactly alike,

but the antennæ of the males differ to a remarkable extent, as was first correctly shown by Leydig.

Similarly in the case of genera there may be observed an incongruence of such a kind that individual parts of the body may deviate to a greater or to a less extent than the corresponding parts in an allied genus. If, for instance, we compare a species of the genus of Daphniacea, *Sida*, with a species of the nearly allied genus *Daphnella*, we find that all the external and internal organs are in some measure dissimilar—nevertheless certain of these parts deviate to an especially large extent, and have without question become far more transformed than the others. This is the case, for example, with the antennæ and the male sexual organs. The latter, in *Daphnella*, open out at the sides of the posterior part of the body as long, boot-shaped generative organs, and in *Sida* as small papillæ on the ventral side of this region of the body. If again we compare *Daphnella* with the nearly allied genus *Latona*, it will be found that no part in the one is exactly similar to the corresponding part in the other genus, whilst certain organs differ more widely than others. This is the case for instance with the oar-like appendages which in *Latona* are triramous, but in *Daphnella*, as in almost all the other Daphniacea, only biramous.

In families the estimation of the form-divergence

of the systems of organs and parts of the body becomes difficult and uncertain: still it may safely be asserted that the two Cladocerous families *Polyphemidæ* and *Daphniidæ* differ much less from one another in the structure of their oar-like appendages than in that of their other parts, such as the head, shell, legs, or abdominal segments. In systematic groups of a still higher order, *i.e.* in orders, and still more in classes, we might be inclined to consider that all the organs had become modified to an equally great extent. Nevertheless it cannot be conclusively said that the kidneys of a bird differ from those of a mammal to the same extent as do the feathers from mammalian hair, since we cannot estimate the differences between quite heterogeneous things—it can only be stated that both differ greatly. Here also the facts are not such as would have been expected if transformation was the result of an internal developmental force; no uniform modification of *all* parts takes place, but first one part varies (variety) and then others (species), and, on the whole, as the systematic divergence increases all parts become more and more affected by the transformation and all tend continually to appear changed to an equal extent. This is precisely what would be expected if the transforming impulses came from the environment. An equalization of the differences caused by transformation must be produced in two ways; first by correlation,



since nearly every primary transformation must entail one or more secondary changes, and secondly because, as the period of time increases, more numerous parts of the body must become influenced by primary transforming factors.

A tempting theme is here also offered by attempting to trace the inequality of phyletic development to dissimilar external influences, and by demonstrating that individual organs have as a rule become modified in proportion to the divergence in the conditions of life by which they have been influenced, this action, during a given period of time, having been more frequent in the case of one organ than in that of the others, or, in brief, by showing the connection between the causes and effects of transformation.

It would be quite premature, however, to undertake such a labour at present, since it will be long before physiology is able to account for the fine distinctions shown by morphology, and further because we have as yet no insight into those internal adjustments of the organism which would enable us *à priori* to deduce definite secondary changes from a given primary transformation. But so long as this is impossible we have no means of distinguishing correlative changes from the primary modifications producing them, unless they happen to arise under our observation.

## APPENDIX I.<sup>1</sup>

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### ADDITIONAL NOTES ON THE ONTOGENY, PHYLOGENY, &c., OF CATERPILLARS.

*Ontogeny of the Noctua larvæ.*—References have already been given in a previous note (2, p. 166) to observations on the number of legs and geometer-like habits of certain *Noctua*-larvæ when newly hatched. This interesting fact in the development of these insects furnishes a most instructive application of the principle of ontogeny to the determination of the true affinities, *i. e.* the blood-relationship of certain groups of Lepidoptera. While the foregoing portions of this work have been in course of preparation for the press, some additional observations on this subject have been published, and I may take the present opportunity of pointing out their systematic bearing—not, indeed, with a view to settling definitively the positions of the groups in question, as our knowledge is still somewhat scanty—but with the object of stimulating further investigation.

Mr. H. T. Stainton has lately recorded the fact that the young larva of *Triphæna Pronuba* is a semi-looper (Ent. Mo. Mag. vol. xvii. p. 135); and in a recently published life-history of *Euclidia Glyphica* (*Ibid.* p. 210) Mr. G. T. Porritt states that this caterpillar is a true looper when young, but becomes a semi-looper when adult. To these facts Mr. R. F. Logan adds (*Ibid.* p. 237) that “nearly all the larvæ of the *Trifidæ* are semi-loopers when first hatched.” The *Cymatophoræ*

<sup>1</sup> By the Editor.

appear to be an exception, but Mr. Logan points out that this genus is altogether aberrant, and seems to be allied to the *Tortricidæ*. Summing up the results of these and the observations previously referred to, it will be seen that this developmental character has now been established in the case of species belonging to the following families of the section *Genuinæ*:—*Leucaniidæ*, *Apameidæ*, *Caradrinidæ*, *Noctuidæ*, *Orthosiidæ*, *Hadenidæ*, and *Xylinidæ*, as well as the other *Trifidæ* (excepting *Cymatophora*).<sup>2</sup> The larvæ of the *Minores* and *Quadridæ* are as a rule semi-loopers when adult and may be true loopers when young, although further observations on this point are wanted. These facts point to the conclusion that the *Noctuæ* as a whole are phyletically younger than the *Geometræ*, whilst the *Genuinæ* and *Bombyciformes* have further advanced in phyletic development than the *Minores* and *Quadridæ*. The last two sections are therefore the most closely related to the *Geometræ*, as correctly shown by the arrangement given in Stainton's "Manual," whilst that adopted in Doubleday's "Synonymic List," where the *Geometræ* precede the *Noctuæ*, is most probably erroneous.

*Additional descriptions of Sphinx-larvæ*.—In the foregoing essay on "The Origin of the Markings of Caterpillars," Dr. Weismann has paid special attention to the larvæ of the *Sphingidæ* and has utilized for this purpose, in addition to his own studies of the ontogeny of many European species, the figures in the chief works dealing with this family published down to the time of appearance of his essay (1876).<sup>3</sup> In order to amplify this part

<sup>2</sup> Mr. C. V. Riley in his excellent "Annual Reports" already quoted in previous notes, states that the larvæ of *Agrotis Inermis*, *Leucania Unipuncta* (Army-worm), and *L. Albilinea* are all loopers when newly hatched. (See First Report, p. 73; Eighth Report, p. 184; and Ninth Report, p. 53.)

<sup>3</sup> The following species not referred to in the previous part

of the subject I have added references to more recent descriptions and figures of Sphinx-larvæ published by Burmeister and A. G. Butler, and I have endeavoured in these cases to refer the caterpillars as far as possible to their correct position in the respective groups founded on the ontogeny and phylogeny of their allies. It is, however, obvious that for the purposes of this work figures or descriptions of adult larvæ are of but little value, except for the comparative morphology of the markings; and even this branch of the subject only becomes of true biological importance when viewed in the light of ontogeny. As our knowledge of the latter still remains most incomplete in the case of exotic species, it would be at present premature to attempt to draw up any genealogy of the whole family, and I will here only extend the subject by adding some few descriptions of species which are interesting as having been made from the observations of field-naturalists, and which contain remarks on the natural history of the insects.

Mr. C. V. Riley in his "Second Annual Report on the Noxious, Beneficial, and other Insects of the State of Missouri, 1870," gives figures and describes the early

of this work are figured by Semper (Beit. zur Entwicklungsgeschichte einiger ostasiat. Schmet.; Verhandl. d. k.k. zoo. bot. Gesell. in Wien, 1867):—*Panacra Scapularis*, Walk.; *Cherocampa Clotho*, Drury; and *Diludia (Macrosila) Discistriga*, Walk. The following are figured by Boisduval and Guenée. (Spéc. Gén. 1874):—*Smerinthus Ophthalmicus*, Boisd.; *Sphinx Jasminearum*, Boisd.; *S. (Hyloicus) Plebeia*, Fabr.; *S. (Hyloicus) Cupressi*, Boisd.; *S. (Pseudosphinx) Catalpæ*, Boisd.; *Philampelus Jussieuæ*, Hübn. (= *Sphinx Vitis*, Linn. ?); and *Ceratonia Amyntor*, Hübn. As the works of Abbot and Smith, and Horsfield and Moore have been exhausted by Dr. Weismann, it is quite unnecessary to extend this note by giving a list of the species figured by these authors.



stages and adult forms of certain grape-vine feeding larvæ of the subfamily *Chærocampinæ*. The full-grown larva of *Philampelus Achemon*, Drury, "measures about  $3\frac{1}{2}$  inches when crawling, which operation is effected by a series of sudden jerks. The third segment is the largest, the second but half its size, and the first still smaller, and when at rest the two last-mentioned segments are partly withdrawn into the third. . . . The young larva is green, with a long slender reddish horn rising from the eleventh segment and curving over the back." Mr. Riley then states that full grown specimens are sometimes found as green as the younger ones, but "they more generally assume a pale straw or reddish-brown colour, and the long recurved horn is invariably replaced by a highly polished lenticular tubercle." The specimen figured was the pale straw variety, this colour deepening at the sides, and finally merging into a rich brown. The markings appear to consist of an interrupted brown dorsal line, a continuous subdorsal line of the same colour, and six oblique scalloped white bars along the side. Whether the colour and marking is adapted to the vine, as is the case with the two varieties of the dimorphic *Chærocampa Capensis* (q.v.), is not stated. The larva of *Philampelus Satellitia*, Linn., when newly hatched, and for some time afterwards is "green with a tinge of pink along the sides, and with an immensely long straight pink horn at the tail. This horn soon begins to shorten, and finally curls round like a dog's tail." The colour of the insect changes to a reddish-brown as it grows older, and the caudal horn is entirely lost at the third moult. The chief markings appear to be five oblique cream-yellow patches with a black annulation on segments 6—10, and a pale subdorsal line. The caterpillar crawls by a series of sudden jerks, and often flings its "head savagely from side to side when alarmed." "When at rest, it draws back the fore part of the body and retracts the

head and first two joints into the third." Two points in connection with these species are of interest with respect to the present investigations. The green colour and the possession of a long caudal horn when young shows that these larvæ, like those of *Chærocampa Elpenor* (p. 178), *C. Porcellus* (p. 184), and *Philampelus Labruscæ* (p. 195, note), are descended from ancestors which possessed these characters in the adult state.<sup>4</sup> The next point of interest is the attitude of alarm assumed by these larvæ, and effected by withdrawing the head and two front segments into the third.<sup>5</sup> The importance of this in connection with the similar habit of ocellated species will be seen on reading the remarks on page 367 bearing upon the initial stages of eye-spots. The other species figured by Mr. Riley are *Chærocampa Pampinatrix*, Smith and Abbot, and *Thyreus Abboti*, Swains. The latter has already been referred to (p. 256).

In a paper "On a Collection of Lepidoptera from Candahar" (Proc. Zoo. Soc., May 4th, 1880), Mr. A. G. Butler has described and figured, from materials furnished to him by Major Howland Roberts, the larvæ of three species of *Sphingidæ*. *Chærocampa Cretica*, Boisd., feeds on vine; out of 100 specimens examined, there was not one black variety, while in another closely allied species, found at Jutogh and Kashmir, the larva is stated to be as often black as green. The general colour of the caterpillar harmonizes with that of the under side of the vine leaves; it possesses a thread-like dorsal, and a pale yellow subdorsal line; also "a subdorsal row of eye-spots, each consisting of a green patch in a yellow oval, the first spot on the fifth segment being the largest and most distinct, those on each following segment

<sup>4</sup> The same inference has already been drawn with respect to *Pterogon* (*Proserpinus*) *Ænotheræ*, see pp. 257, 258.

<sup>5</sup> This would of course be the *fourth* segment if the head be considered the first, as on the Continent.

becoming smaller, more flattened, and less distinct, till lost on the twelfth segment, sometimes becoming indistinct after the seventh or eighth segment ; these spots are only distinct as eye-spots on the fifth and sixth segments, that on the sixth being flatter than that on the fifth, those on the remaining segments appearing like dashes while the larvæ is green, but more like eyes on its changing colour when full fed." The change here alluded to is the dark-brown coloration so generally assumed by green Sphinx-larvæ previous to pupation, and which, as I have stated elsewhere (Proc. Zoo. Soc., 1873, p. 155), is probably an adaptation advantageous to such larvæ when crawling over the ground in search of a suitable place of concealment. Making the necessary correction for the different mode of counting the segments, it will be seen that the primary ocelli of this species are in the same position as those of the other species of this genus as described in a previous part of this essay, and that it belongs to the second phyletic group treated of at p. 193. The interesting fact that this species does not display dimorphism, whilst the closely allied form from Kashmir is dimorphic, shows that in the present species the process of double adaptation has not taken place ; and this will probably be found to be connected with the habits of life, *i. e.* the insect being well adapted to the colour of its food-plant may not conceal itself on the ground by day. The caterpillar of *Deilephila Robertsii*, Butl., is found at Candahar on a species of *Euphorbia* growing on the rocky hills, and is so abundant that at the end of May every plant with any leaves left on it had several larvæ feeding upon it. "The larvæ are very beautiful and conspicuous, and are very different in colouring according to their different stages of growth." The general colour is black with white dots and spots ; a subdorsal row of large roundish spots, one on each segment, either white, yellow, orange or

red; dorsal stripe variable in colour, and sometimes only partially present or altogether absent. "At the end of May most of the larvæ found presented a different appearance; the black disappears more or less, and with it many of the small white spots. In some cases the black only remains as a ring round the larger white spots; the ground-colour therefore becomes yellowish-green or yellow, varying very considerably." The larva does not change colour previous to pupation. This species, according to the outline figure given (*loc. cit.*, Pl. XXXIX., Fig. 9), appears to belong to the first of Dr. Weismann's groups, comprising *D. Euphorbiæ*, *D. Dahlii* and *D. Nicæa* (see p. 199), and is therefore in the seventh phyletic stage of development (p. 224). From the recorded habits it seems most probable that the colours and markings of this caterpillar are signals of distastefulness. It is much to be regretted that Major Roberts has not increased the value of his description of this species by adding some observations or experiments bearing on this point. *Eusmerinthus Kindermanni*, Lederer, feeds on willow. "General colour green, covered with minute white dots and seven long pale-yellow oblique lateral bands. (The ground-colour is the same as the willow-leaves on which the larva feeds, the yellow stripes the same as the leaf-stalks, and the head and true legs like the younger branches)." As no subdorsal line is mentioned or figured, this species must be regarded as belonging to the third stage of phyletic development (see p. 242).

I have recently had an opportunity of inspecting a large number of drawings of Sphinx-larvæ in the possession of Mr. F. Moore, and of those species not mentioned in the previous portions of this work the following may be noticed:—*Chærocampa Theylia*, Linn., like *Ch. Lewisii* (note 13, p. 194), appears to be another form connecting the second and third phyletic groups of



this genus. *Ch. Clotho*, Drury, belongs to the third group (figured by Semper ; see note 3 to this Appendix). The larva of *Ch. Lucasii*, Walk., offers another instance of the retention of the subdorsal line by an ocellated species. The larva of *Ch. Lycetus*, Cram., of which Mr. Moore was so good as to show me descriptions made at the various stages of growth, presents many points of interest. It belongs to the third phyletic group, and all the ocelli appear at a very early stage. The dimorphism appears also in the young larvæ, some being green, and others black, a fact which may be explained by the law of "backward transference" (see p. 274). A most suggestive feature is presented by the caudal horn, which in the young caterpillar is stated to be *freely movable*. It is possible that this horn, which was formerly possessed by the ancestors of the *Sphingidæ*, and which is now retained in many genera, is a remnant of a flagellate organ having a similar function to the head-tentacles of the *Papilio*-larvæ, or to the caudal appendages of *Dicranura* (see p. 289).

*Lophostethus Dumolinii*, Angas.—The larva of this species differs so remarkably from those of all other *Sphingidæ*, that I have thought it of sufficient interest to publish the following description, kindly furnished by Mr. Roland Trimen, who in answer to my application sent the following notes :—" My knowledge of the very remarkable larva of this large and curious Smerinthine Hawk-moth is derived from a photograph by the late Dr. J. E. Seaman, and from drawings and notes recently furnished by Mr. W. D. Gooch. The colour is greenish-white, inclining to grey, and in the male there is a yellow, but in the female a bluish, tinge in this. All the segments but the second and the head bear strong black spines, having a lustre of steel blue, and springing from a pale yellow tubercular base. The longest of these spines are in two dorsal rows from the fourth to the

eleventh segment, the pairs on the fourth and fifth segments being longer than the rest, very erect, and armed with short simple prickles for three-fourths of their upper extremity. The anal horn, which is shorter than the spines, is of the same character as the latter, being covered with prickles, and much inclined backwards. Two lateral rows of similar shorter spines extend from the fourth to the 12th segment, and on each of the segments 6—11 the space between the upper and lower spines is marked with a conspicuous pale yellow spot. Two rows of smaller similar spines extend on each side (below the two rows of larger ones) from the second to the thirteenth segment, one spine of the lowermost row being on the fleshy base of each pro-leg. All the pro-legs are white close to the base, and russet-brown beyond. Head smooth, unarmed in adult, greenish-white with two longitudinal russet-brown stripes on face.

“The young larvæ have proportionally much longer and more erect spines with distinct long prickles on them. There is a short pair besides, either on the back of the head or on the second segment. Moreover, the dorsal spines of the third and fourth segments, and the anal horn (which is quite erect, and the longest of all), are longer than the rest, and distinctly *forked* at their extremity.

“Mr. Gooch notes that these young larvæ might readily be mistaken for those of the *Acrææ*, and suggests that this may protect them. He also states that the yellow lateral spots are only noticed after the last moult before pupation, and that the general resemblance of the larva as regards colour is to the faded leaves of its food-plant, a species of *Dombeya*.”

The forked caudal horn in the young larva of this species is of interest in connection with the similar character of this appendage in the young caterpillar of *Hyloicus Pinastris*, p. 265.

*Retention of the Subdorsal Line by Ocellated Larvæ.*—It has already been shown with reference to the eye-spots of the *Cherocampa*-larvæ, that these markings have been developed from the subdorsal line, and that, in accordance with their function as a means of causing terror, this line has in most species been eliminated in the course of the phylogeny from those segments bearing the eye-spots in order to give full effect to the latter (see p. 379). In accordance with the law that a character when it has become useless gradually disappears, the subdorsal is more or less absent in all those species in which the ocelli are most perfectly developed; and it can be readily imagined that in cases where adaptation to the foliage exists the suppression of this line would under certain conditions be accelerated by natural selection. On the other hand, it is conceivable that the subdorsal line may under other conditions be of use to a protectively coloured ocellated species by imitating some special part of the food-plant, under which circumstances its retention would be secured by natural selection.

Such an instance is offered by *Cherocampa Capensis*, Linn.; and as this case is particularly instructive as likewise throwing light upon the retention of the subdorsal by certain species having oblique stripes (see p. 377, and note 7, p. 378), I will here give some details concerning this species which have been communicated to me by Mr. Roland Trimen, the well-known curator of the South African Museum, Cape Town. The caterpillar of *C. Capensis*, like so many other species of the genus, is dimorphic, one form being a bright (rather pale) green, and the other, which is much the rarer of the two, being dull pinkish-red. Both these forms are adapted in colour to the vine on which they feed, the red variety according to some extent with the faded leaves of the cultivated vines, but to a greater extent with the young shoots and under-side of the leaves of the South African native vine (*Cissus*

*Capensis*), on which it also feeds. There are two eye-spots in this species in the usual positions ; they are described as being blue-grey in a white ring, and raised so as to project a little. The subdorsal is white, and is bordered beneath by a wide shade of bluish-green irrorated with white dots, and crossed by an indistinct white oblique ray on each segment. These last markings are probably remnants of an oblique striping formerly possessed by the progenitor of this and other species of the genus (see, for instance, Fig. 25, Pl. IV., one of the young stages of *C. Porcellus*). It is possible that these rudimentary oblique stripes are now of service in assisting the adaptation of the larva to its food-plant, but this cannot be decided without seeing the insect *in situ*.

The subdorsal line extends from immediately behind the second eye-spot to the base of the very short and much curved violet anal horn. With reference to the protective colouring Mr. Trimen writes :—" The difficulty of seeing these large and beautifully-coloured larvæ on the vines is quite surprising ; six or more may be well within sight, and yet quite unnoticed. The subdorsal stripe greatly aids in their concealment, as it well represents in its artificial light and shade the leaf-stalks of the vine." When this larva withdraws its front segments the eye-spots stand out very menacingly ; but in spite of this it is greedily eaten by fowls and shrikes (*Fiscus Collaris*), and Mr. Trimen also found that a tame suricate (*Rhysæna Suricata*) and a large monitor lizard (*Regenia Albogularis*) did not refuse them. The failure of the eye-spots in causing terror in these particular cases cannot be regarded as disproving their utility in all instances. It must always be borne in mind that no protective character can possibly be of service against *all* foes ; natural selection only requires that such characters should be advantageous with respect to the majority of the enemies of any species, and further experiments with



this caterpillar may show that in the case of smaller foes the eye-spots are effective as a means of causing alarm. The dimorphism of the larva of *C. Capensis* is of special interest, although we are not yet sufficiently acquainted with the habits of this species to offer a complete explanation. According to Dr. Weismann's conclusions (p. 297), the dimorphism of the *Chærocampa*-larvæ is due to a double adaptation, the insects first having acquired the habit of concealing themselves by day, and the dark form having then been produced by the action of natural selection, in order to adapt such varieties to the colour of the soil, whilst others retained the green colour which adapts them to the foliage of their food-plants. In accordance with this, *C. Capensis* may have a similar habit of concealment, or (should this be found not to be the case) it is possible that this insect at a former period possessed this habit and fed upon some other plant, when it would have become dimorphic in the manner explained, and the *existing* dimorphism may be a survival of the more ancient dimorphism, the red form (corresponding to the older dark form) having been subsequently modified so as to become also adapted to the new food-plant. Much light would be thrown upon this by studying the ontogeny of the species.

*Phytophagic Variability.*—A number of observations bearing on the phytophagic variability of the Sphinx-larvæ and other caterpillars have been recorded in a previous note (p. 305), and reference has also been made to the food-plants of *Acherontia Atropos* in South Africa (note 50, p. 263). I am now enabled to add some further observations on this species, from notes furnished to me by Mr. Roland Trimen, who states that for many years he has noticed that at the Cape this larva varies greatly in the depth and shade of the green ground-colour, the variability being in strict accordance with the colour of the leaves of the particular plant on which the

individual feeds. The phenomenon was particularly noticeable in larvæ feeding on *Buxia Grandiflora*, a shrub in common cultivation in gardens, and of which the foliage is of a very dull pale greyish-green. Another striking instance was noticed in some very fine caterpillars feeding on a large shrubby *Solanum*, which, excepting the bright yellow bands bordering the dorsal violet bars, were generally dull ochreous-yellow, like the leaves and stalks of the *Solanum*. On plants with bright green or deep green leaves, the colour of the larvæ is almost in exact agreement. Mr. Trimen adds :—"These remarks apply principally to the underside and pro-legs and lower lateral regions, the dorsal colours of violet and yellow varying but little. The protection afforded is very considerable, as the larvæ almost always cling to the lower side of the twigs of their food-plants, so that their uniformly-coloured under-surface is upwards, and turned towards the light, and their variegated upper surface turned downwards."

These observations are of the highest importance, not only as adding another instance to the recorded cases of phytophagic variation, but likewise as showing that with this variability a protective habit has been acquired. It is to be hoped that such a promising field for experimental investigation as is offered by this and analogous cases will not long remain unexplored. In attacking the problem two chief questions have in the first place to be settled : (1) Is the variability truly phytophagic, *i. e.* are the colour-variations actually brought about by the chemico-physiological action of the food-plant? and (2) Are the larvæ at any period of growth susceptible to the action of phytophagic influences? The first question could be decided by feeding larvæ from the same batch of eggs on different food-plants from the period of their hatching. The second question could be settled by changing the food-plants of a series of selected specimens

at various stages of growth, and observing whether any change of colour was produced. In accordance with the principles advocated in a previous note (p. 305), it is conceivable *à priori* that phytophagic variability may occur by direct chemico-physiological action, quite irrespective of any of the changes of colour being of protective use. In the case of brightly-coloured distasteful species phytophagic variability might thus have full play, but in the case of protectively-coloured edible species, phytophagic variability would be under the control of natural selection. These considerations raise a question of the greatest theoretical interest in connection with this phenomenon. If phytophagic variability can have full play uncontrolled by natural selection in brightly-coloured caterpillars, ought not this phenomenon to be of more common occurrence in such species than in those protectively coloured? Although our knowledge of this subject is still very imperfect, as a matter of fact brightly coloured larvæ, so far as I have been able to ascertain, do not appear to be susceptible of phytophagic influences. But this apparent contradiction, instead of opposing actually confirms the foregoing views, as will appear on further consideration. The colours of protected species are as a whole much inferior in brilliancy to those of inedible species, so that any phytophagic effect would be more perceptible in the former than in the latter, in which the highest possible standard of brilliancy appears in most cases to have been attained. Now phytophagic variations of colour appear to be of but small amount, or, in other words, such variations fluctuate within comparatively restricted limits, and as the cases at present known are mostly *adaptive* it is legitimate to conclude that they have been produced and brought to their present standard by natural selection, *i. e.* that they have arisen from phytophagic influences as a cause of variability. The initial stages

of phytophagic variations must therefore have been still less perceptible than the now perfected final results; and this leads to the conclusion that minute variations of this character were of sufficient importance to protectively-coloured species to be taken advantage of by natural selection. But minute variations in a dull-coloured larva would, as previously pointed out, produce a comparatively much greater effect than such variations in a brilliantly-coloured species; and as protection is required by the former, the initial phytophagic effects would be accumulated, and the power of adaptability conferred by the continued action of natural selection, whilst in vividly-coloured species where no power of adaptability is required this cause of variation would not only produce a result which, as compared with its effects upon dull species, may be regarded as a "vanishing quantity," but this result would be too insignificant to be taken advantage of by natural selection, which is in these cases dealing only with large "quantities," and striving to make the caterpillars as brilliant as possible. The fact that vividly-coloured distasteful larvæ do not show phytophagic variation is to my mind explained proximately by these considerations; the ultimate cause of phytophagic variability regarded as a chemico-physiological action requires further investigation.

*Sexual Variation in Larvæ.*—Since most of the markings of caterpillars can be explained by the two factors of adaptation and inheritance, or, in other words, by their present and past relations to the environment, and since sexual selection can have played no direct part in producing these colours and markings, I feel bound to record here some few observations on the sexual differences in larvæ in addition to the cases of *Anapæa* and *Orgyia* already recorded (note i., p. 308) and of *Lophostethus Dumolinii* (p. 527).



Mr. C. V. Riley states<sup>6</sup> with reference to the larva of *Thyreus Abbotti* that the ground-colour appears to depend upon the sex, Dr. Morris having described the insect as "reddish-brown with numerous patches of light green," and having expressly stated that "the female is of a uniform reddish-brown with an interrupted dark-brown dorsal line and transverse striæ." Mr. W. D. Gooch, who has reared the South African butterflies *Nymphalis Cithæron* and *N. Brutus* from their larvæ, states<sup>7</sup> that these "differed sexually in both instances." Of *Brutus* only a few were bred, but of *Cithæron* many. "The sexual difference of the latter was that the females had a large dorsal sub-cordate cream mark, which was wanting, or only shown by a dot, in the males, and the colour was more vivid in the edgings to the frontal horns."

Although such cases appear to be at present inexplicable, they are of interest as examples of those "residual phenomena" which, as is well known, have in many branches of science so often served as important starting-points for new discoveries and generalizations.<sup>8</sup>

<sup>6</sup> "Second Annual Report," 1870, p. 78.

<sup>7</sup> "Entomologist," vol. xiv. p. 7.

<sup>8</sup> With reference to the habits of *C. Capensis* (p. 531), I have since been informed by Mr. Trimen that this species does not conceal itself by day, so that the dimorphism may be regarded as a character retained from an earlier period and adapted to the present life conditions.

## APPENDIX II.

THE following paper by Dr. Fritz Müller<sup>1</sup> forms the third of a series of communications on Brazilian butterflies published in "Kosmos," and as it bears upon the investigations made known in the third essay of the present work, I will here give a translation, by permission of the publisher, Herr Karl Alberts.

### "ACRÆA AND THE MARACUJÁ BUTTERFLIES AS LARVÆ, PUPÆ, AND IMAGINES.

"In a thoughtful essay on 'Phyletic Parallelism in Metamorphic Species,' Weismann has shown that in the case of Lepidoptera the developmental stages of larva, pupa, and imago vary independently, and that a change occurring in one stage is without influence upon the preceding and succeeding stages, so that the course which has been followed by the individual stages in their developmental history has not been in all cases identical. This want of agreement may manifest itself both by unequal divergence of form-relationship, and by unequal group formation. With respect to unequal form-divergence the caterpillars are sometimes more closely related in form than their imagines, and at other times the reverse is the case. With respect to unequal group formation again, two cases are possible; the larvæ and imagines may form groups of unequal value, the one stage form-

<sup>1</sup> "Kosmos," Dec. 1877, p. 218. The paper is here introduced chiefly with a view to illustrate an important case of incongruence among Lepidopterous pupæ.

ing higher or lower groups than the other, or they may form groups of unequal size, *i. e.*, groups which do not coincide but which overlap. Form-relationship and blood-relationship do not therefore always agree; the resemblances among the caterpillars would lead to a quite different arrangement to that resulting from the resemblances among the imagines, and it is probable that neither of these arrangements would correspond with the actual relationships.

"Starting from this fact, which he establishes by numerous examples, Weismann proceeds to show most convincingly that an innate power of development or of transformation, such as has been assumed under various names by many adherents of the development theory, has no existence, but that every modification and advancement in species has been called forth by external influences.

"A most beautiful illustration of the want of 'phyletic parallelism,' as Weismann designates the different form-relationships of the larvæ, pupæ, and imagines, is furnished by the five genera *Acræa*, *Heliconius*, *Eueides*, *Colænis*, and *Dione* (= *Agraulis*). This instance seems to me to be of especial value, because it offers the rare case of pupæ showing greater differences than the larvæ and imagines.

"The species of which I observed the larvæ and pupæ are *Acræa Thalia* and *Alalia*, *Heliconius Eucrate*, *Eueides Isabella*, *Colænis Dido* and *Julia*, *Dione Vanillæ* and *Juno*; besides these I noticed the pupa of *Eueides Aliphera*.

"The following remarks apply only to these species, although we may suppose with great probability that the whole of the congeneric forms—excepting perhaps the widely ranging species of *Acræa*—would display similar characters to their Brazilian representatives.

"The imagines of the five genera mentioned form two

sharply defined families, the *Acræidæ* and the butterflies of the Maracujá group.<sup>2</sup> The latter comprises the three genera *Heliconius*, *Eucides*, and *Colænis*, which differ only in very unimportant characters; *Eueides* is distinguished from *Heliconius* by its shorter antennæ, and *Colænis* differs from *Eueides* in having the discoidal cell of the hind-wings open. The genus *Dione* is further removed by the different structure of the legs, and the silvery spots on the underside of the wings. Certain species resemble those of other genera in a most striking manner, and much more closely both in colour and marking, and even in the form of their wings, than they do their own congeners. This is the case with *Acræa Thalia* and *Eucides Pavana*, with *Heliconius Eucrate* and *Eucides Isabella*, and with *Eueides Aliphera* and *Colænis Julia*, which are deceptively alike, and the last two are connected with *Dione Juno*, at least by the upper side of the wings. The difficulty of judging of the relationships of the single species is thus much aggravated; it cannot be said how much of this resemblance is to be attributed to blood-relationship, and how much to deceptive imitation.

"As larvæ all the Brazilian species must be placed in one genus, as they agree exactly in the number and arrangement of their spines (4 spines, not in a transverse row, on segments 2 and 3; 6 spines, in a transverse row, on segments 4—11; 4 spines, not in a transverse row, on the last (12th) segment). They differ from one another much less in this respect than do the German species of *Vanessa*, such, for instance, as *V. Io* or *Antiopa* from *V. Polychloros*, *Urticæ*, and *Atalanta*.<sup>3</sup> The larvæ of *Acræa Thalia* are certainly without the two spines on the head which the others possess, and, on the other hand, they have a well-developed pair of spines on the

<sup>2</sup> [Maracujá, the local name for the Passiflora. R.M.]

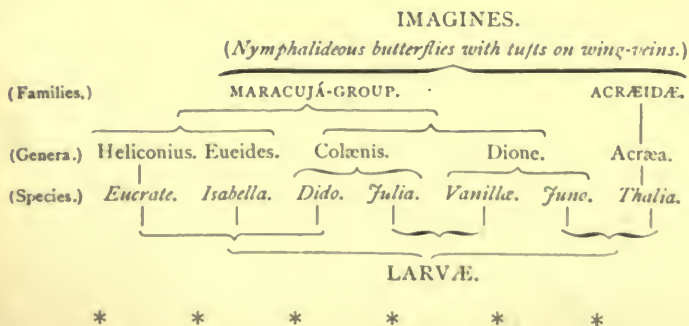
<sup>3</sup> See p. 448.



first segment, which, in most of the other species, are completely absent; but this does not justify their separation, since the head spines of *Heliconius*, *Eueides*, and *Colænis Dido*, which are of a considerable length, are shorter than those of the next segment in *Colænis Julia*, and *Dione Vanilla*, and in *Dione Juno* they dwindle down to two minute points, this last species also bearing a short pair on the first segment. The larva of *Dione Juno* is thus as closely related to that of *Acræa Thalia* as it is to that of its congener *Dione Vanilla*.

"If it were desired to form two distinct larval groups this could not be effected on the basis of their differences in form, but could only be based on their food-plants. The larvæ of *Heliconius*, *Eueides*, *Colænis*, and *Dione* live on species of Maracujá (*Passiflora*); those of *Acræa Thalia* and *Alalia* on Compositæ (*Mikania* and *Veronia*). These larval groups would agree with those founded on the form-relationships of the imagines, but unlike the imaginal groups, which can be formed into families, they would scarcely possess a generic value.

"If we arrange the single species of caterpillars according to their resemblances, this arrangement does not agree with that based on the resemblances of the imagines, even if we disregard the different values of the groups. The result is somewhat as follows:—



[Here follow the remarks on the habits of the larvæ in connection with their colours, &c., which have already been quoted in illustration of the use of the spiny protection (note 5, p. 293). From these facts the author draws the conclusion that the form-relationships of the caterpillars depend rather upon their mode of life than upon their blood-relationships, assuming the latter to be correctly expressed by the arrangement of the imagines at present adopted.]



Fig. 1.



Fig. 2.



Fig. 3



Fig. 4.

Figs. 1—4. Pupæ of *Acræa Thalia*; *Heliconius Eucrate*; *Eueides Isabella*, and *Colænis Dido*; life size.

“A glance at the above figures of the pupæ of *Heliconius Eucrate* (Fig. 2), *Eueides Isabella* (Fig. 3), and *Colænis Dido* (Fig. 4), will show how great are the differences between these pupæ as compared with the close form-relationship of all the Maracujá butterflies, and with the no less close resemblance of their larvæ. A family which comprised three such dissimilar pupæ would also be capable of including that of *Acræa Thalia* (Fig. 1).

"The pupa of this last species has nothing peculiar in its general appearance, but possesses the ordinary pupal form ; it is tolerably rounded, without any great elevations or depressions ; a minute pointed projection is situated on the head over each eye-cover, and a similar process projects from the roots of the wings. Its distinguishing characters are five pairs of spines on the back of the abdominal segments. These spines are found also in *Acræa Alalia*, but appear to be absent in other species, e.g. in the Indian *A. Viola*. Last summer, among some batches of *Thalia* larvæ—each batch being the progeny from one lot of eggs—I found certain individuals which differed from the others in having much shorter spines, and these changed into pupæ in which the five pairs of spines were proportionally shorter than usual, thus being an exception to the rule that changes in one stage of development are without influence on the other stages. I may remark, by the way, that this law, enunciated by Weismann, can only be applied to imagines and pupæ with certain restrictions. The skin of the pupa forms a sheath or cover for the eyes, antennæ, trunk, legs, and wings of the imago, and if these parts undergo any considerable modification in the latter, corresponding changes must appear in the pupa. This is shown, for instance, by many 'Skippers' (*Hesperidæ*), in which the extraordinarily long trunk necessitates a sheath of a corresponding length. The colour of the pupa of *Acræa Thalia* is whitish, the wing-veins with some other markings and the spines are black ; metallic spots are absent.

"In the pupa of *Heliconius Eucrate* the laterally compressed region of the wings is raised into a large projection, the antennal sheaths lying on the edges of the wings are serrated and beset with short pointed spines ; instead of the minute projections of *Acræa Thalia*, the head bears two large humped processes ; the body is

raised on each side into a foliaceous border carrying five spines of different lengths, the foremost pair, directed towards the head, being the longest. The pupa is brown, and ornamented with four pairs of brilliant metallic spots, one pair close behind the antennæ, and three pairs, almost coalescent, on the back before the longest pair of spines. A short spine projects from the middle of each of the latter somewhat arched metallic patches.

“ In the pupa of *Colænis Dido* (which resembles that of *Colænis Julia*, and to which may be added those of *Dione Vanilla* and *Juno*) the spines are absent, the wing region is but moderately arched, and the antennæ marked only by small elevations; instead of the leaf-like border, there are on each side of the back five knotty or humped processes. The metallic spots are similar in number and position to those of *Heliconius Eucrate*; those on the back have a wart-like process in the middle, instead of a spine.

“ The pupæ of *Heliconius* and *Colænis* when moving their posterior segments rapidly, as they do whenever they are disturbed, produce a very perceptible hissing noise by the friction of these segments, this sound, which is especially noticeable in the case of *Heliconius Eucrate*, perhaps serving to terrify small foes. (So loud is the sound produced in this manner by the pupæ of *Epicalia Numilia*, that my children have named them ‘*Schrei-puppen*.’)

“ The pupæ of *Heliconius* and *Colænis* thus differ to a much greater extent than the imagines or larvæ, and the same holds good for *Eucides* in a much higher degree as compared with its above-mentioned allies. The larvæ of *Eucides* have no distinctive characters, and even the generic rank of the imagines is doubtful; as pupæ, on the other hand, they are far removed (even by their mode of suspension) not only from the remainder



of the Maracujá group and from the whole of the great Nymphalideous group (*Danainæ*, *Satyrinæ*, *Elymniinæ*, *Brassolinæ*, *Morphinæ*, *Acræinæ* and *Nymphalinæ*), but from almost all other butterflies. The larva pupates on the underside of a leaf; the pupa is fastened by the tail, but does not hang down like the pupæ of the other *Nymphalidæ*,—its last segments are so curved that the breast of the chrysalis is in contact with the underside of the leaf. I am not acquainted with any other pupa among those not suspended by a girdle which assumes such a position. Something similar occurs, however, in the pupa of *Stalachtis*, which is without a girdle, and according to Bates, is 'kept in an inclined position by the fastening of the tail.' By this peculiarity Bates distinguishes the *Stalachtinæ* from the *Libytheæ* with pupæ 'freely suspended by the tail.'

"Besides through this peculiar position of the body, the pupa of *Eueides Isabella* is distinguished by short hooked and long narrow sabre-like pairs of processes on the back and head. Its colour is whitish, yellowish, or sordid yellowish-grey; in the last variety both the four long dorsal processes and the surrounding portions, as well as the points of the other processes, remain white or yellowish. The pupa *Eueides Aliphera* is very similar, only all the processes are somewhat shorter, the four longest (dorsal) and some other markings being black.

"Now if, as Weismann has attempted to show for larvæ and imagines, the form-divergence always 'corresponds exactly with the divergence in the mode of life,' the question arises as to what difference in the conditions of life has brought about such a considerable form-divergence between the pupæ of such closely-allied species as the Maracujá butterflies. In pupæ which do not eat or drink, and which have neither to seek in courtship nor to care for progeny, it is only protection from foes that

can concern us. But in the pupæ of nearly-allied species of which the larvæ feed on kindred plants in the same districts at the same periods of the year, can the enemies be so different as to produce such a considerable divergence in form? One might answer this question in the negative with some confidence, and affirm that in this case the difference in the pupæ does not result from the 'divergence in the mode of life,' or from the difference in the external conditions, but is accidental, *i.e.* a consequence of some fortunate variation induced by some external cause, which variation afforded protection against common foes—to one species in one way, and to the other species in some other way; this course, once entered upon, having been urged on by natural selection, until at length the wide divergence now shown is attained. How in the case of any of the species the peculiarity in colour or form can actually serve as a protection, I must confess myself at fault in answering. Only in the case of the pupa of *Eueides Isabella* will I venture to offer a supposition. That it is not green like other pupæ which suspend themselves among foliage (*Siderome*, *Epicalia*, *Callidryas*, &c.), but contrasts more or less brightly with the dark green of the leaves, precludes the idea of concealment; on the other hand its colour is too dull to serve as a conspicuous sign of distastefulness. In either case the meaning of the wonderful processes of the pupa would remain unexplained.

"We are thus compelled to seek another possibility in mimicry, by which foes would be deceived by deceptive resemblance. But what is the object imitated? Dead insects overgrown by fungi are often found on leaves, the whitish or yellowish fungi growing from their bodies in various fantastic forms. Such insects of course no longer serve as tempting morsels. The processes of the pupa of *Eueides* suggest such fungoid growths, although I cer-

tainly cannot assert that to our eyes in broad daylight the resemblance is very striking. But the pupæ hang among the shadows of the leaves, and a less perfect imitation may deceive foes that are not so sharp-sighted; protective resemblance must commence moreover with an imperfect degree of imitation."

## EXPLANATION OF THE PLATES.

### PLATE III.

Figs. 1—12 represent larvæ of *Macroglossa Stellatarum*, all bred from one batch of eggs. Most of the figures are enlarged, but sometimes to a very small extent only; the lines show the natural length.

Fig. 1. Stage I.; a caterpillar immediately after hatching. Natural length, 0.2 centim.

Fig. 2. Stage II.; shortly after the first moult. Natural length, 0.7 centim.

Figs. 3—12. Stage V.; the chief colour-varieties.

Fig. 3. The only lilac-coloured specimen in the whole brood. Natural length, 3.8 centim.

Fig. 4. Light-green form (rare) with subdorsal shading off beneath.

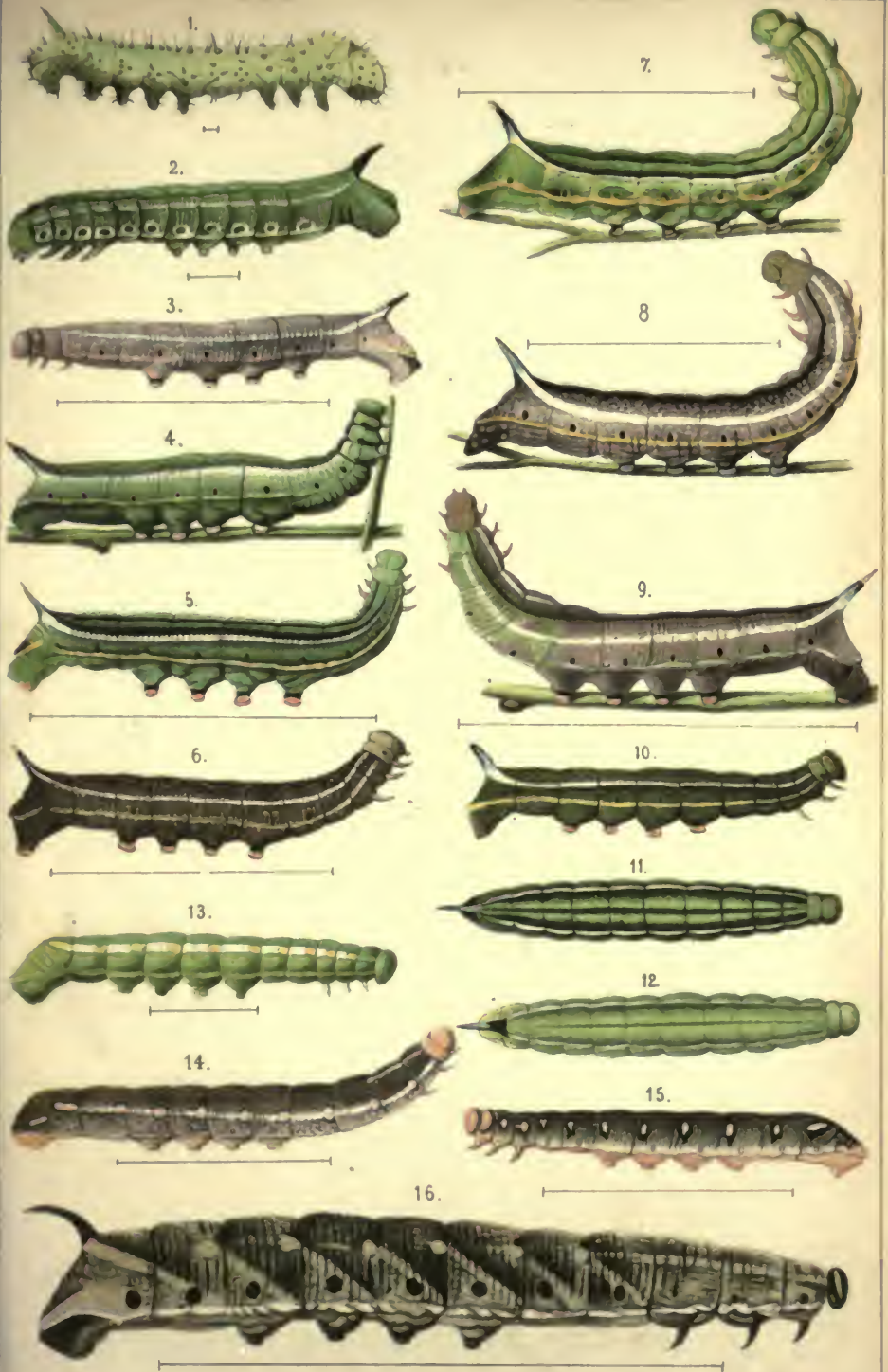
Fig. 5. Green form (rare) with strongly-pronounced dark markings (dorsal and subdorsal lines). Natural length, 4.9 centim.

Fig. 6. Dark-brown form (common). Natural length, 4 centim. In this figure the fine shagreening of the skin is indicated by white dots; in the other figures these are partially or entirely omitted, being represented only in Figs. 8 and 10.

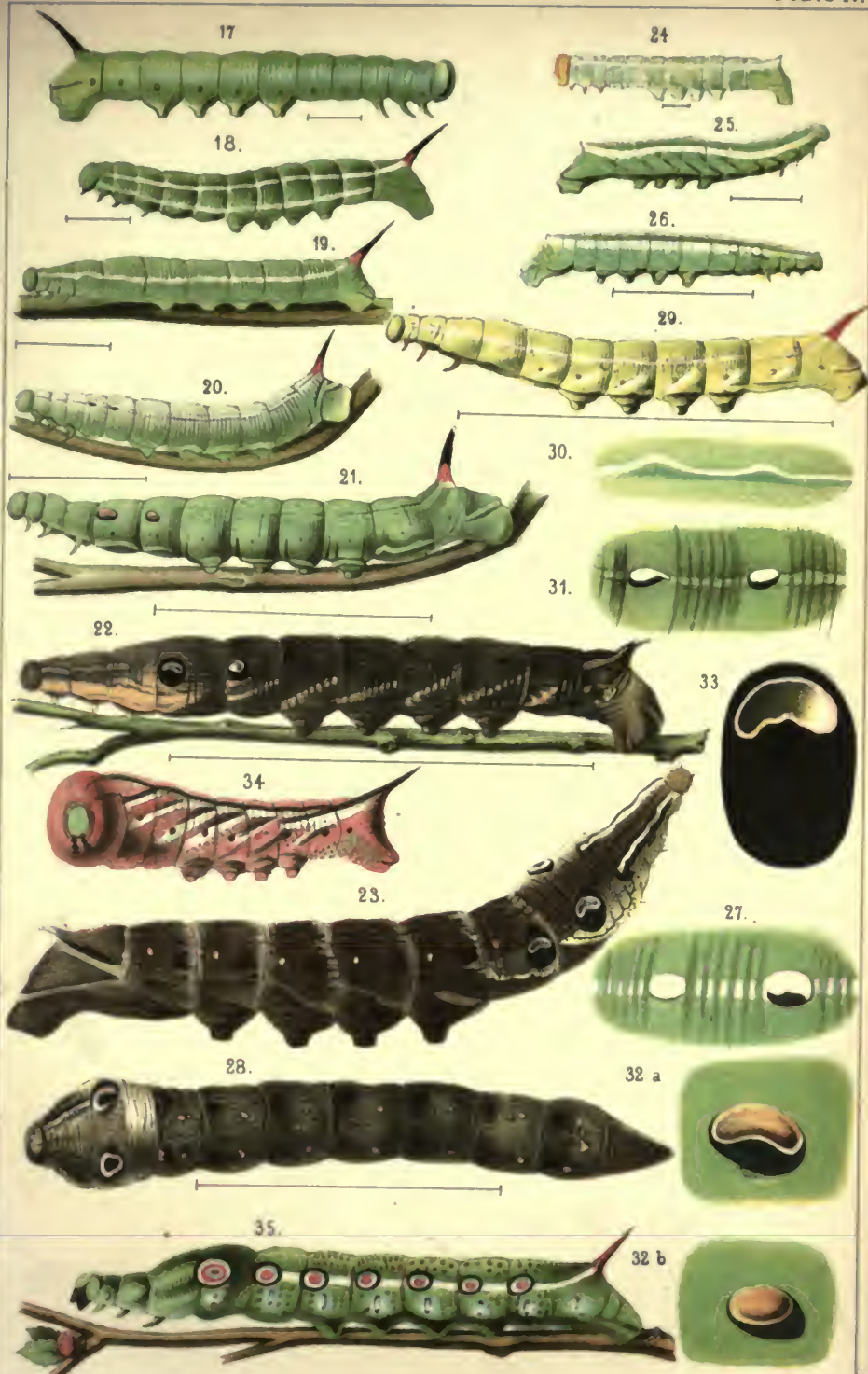
Fig. 7. Light-green form (common). Natural length, 4 centim.

Fig. 8. Light-brown form (common). Natural length 3.5 centim.



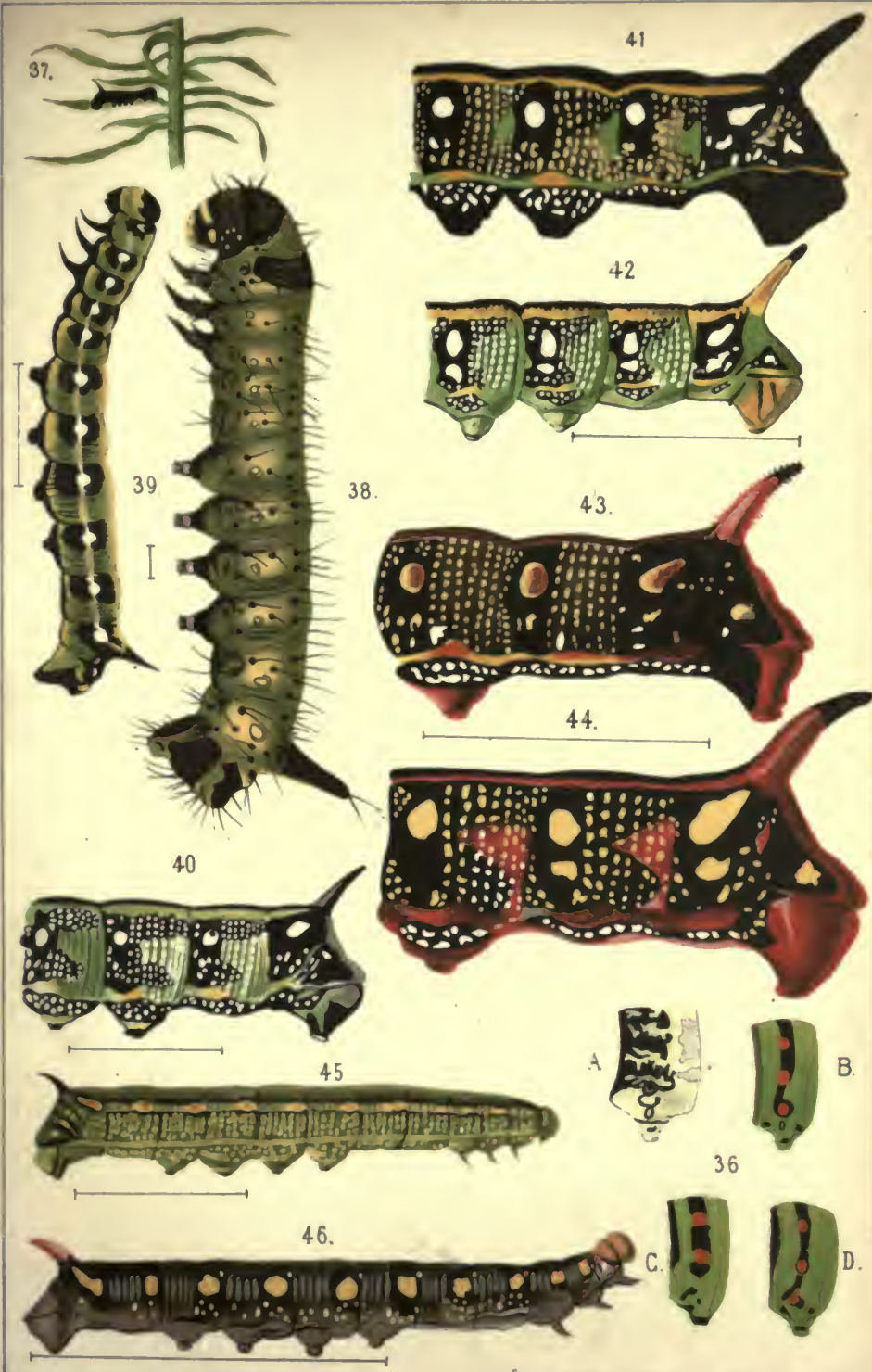














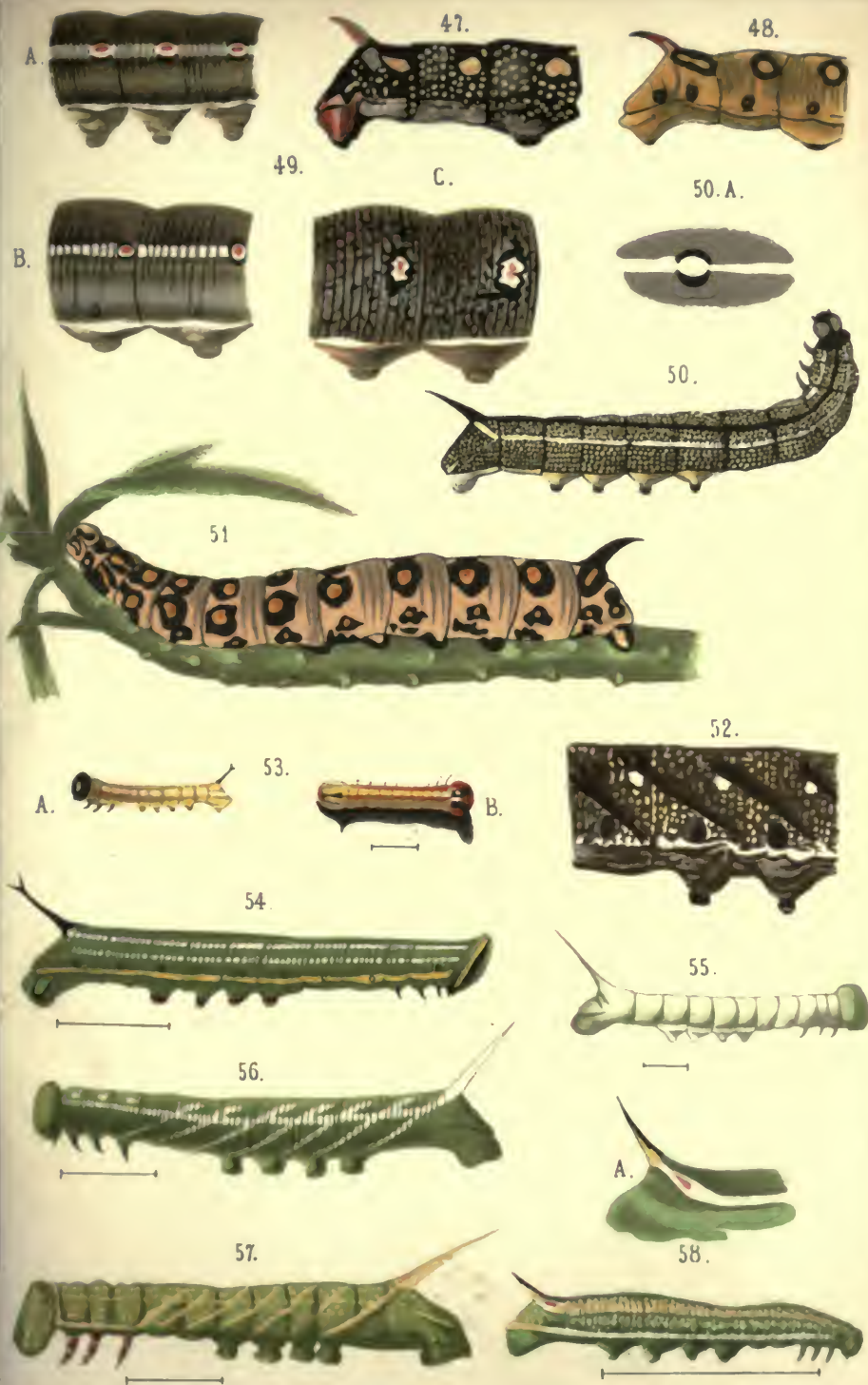






Fig. 9. Parti-coloured specimen, the only one out of the whole brood. Natural length, 5.5 centim.

Fig. 10. Grey-brown form (rare).

Fig. 11. One of the forms intermediate between the dark-brown and green varieties, dorsal aspect.

Fig. 12. Light-green form with very feeble dorsal line (shown too strongly in the figure), dorsal aspect.

Figs. 13—15. *Deilephila Vespertilio*.

Fig. 13. Stage III. (?) ; the subdorsal bearing yellow spots. Natural length, 1.5 centim.

Fig. 14. Stage IV. ; the subdorsal interrupted throughout by complete ring-spots, the white "mirrors" of which are bordered with black, and contain in their centres a reddish nucleus. Natural length, 3 centim.

Fig. 15. Stage V. ; shortly after the fourth moult. Subdorsal line completely vanished ; ring-spots somewhat irregular, with broad black borders ; natural length, 3.5 centim.

Fig. 16. *Sphinx Convolvuli*, Stage V., brown form. Subdorsal line retained on segments 1—3, on the other segments present only in small remnants ; at the points where the (imaginary) subdorsal crosses the oblique stripes there are large bright spots ; natural length, 7.8 centim.

#### PLATE IV.

Figs. 17—22. Development of the markings in *Cherocampa Elpenor*.

Fig. 17. Stage I. ; larva one day after hatching. Natural length, 7.5 millim.

Fig. 18. Stage II. ; larva after first moult. Length, 9 millim.

Fig. 19. Stage II. ; immediately before the second moult (Fig. 30 belongs here). Length, 13 millim.

Fig. 20. Stage III. ; after second moult. Length, 20 millim.

Fig. 21. Stage IV. ; after third moult (Figs. 32 and 33 belong here). Length, 4 centim.

Fig. 22. Stage V. ; after fourth moult. A feeble indication of an eye-spot can be seen on the third segment besides those on the fourth and fifth. Ocelli absent on segments 6—10.

Fig. 23. Stage VI. ; after fifth moult. The subdorsal line is feebly present on segments 6—10, and very distinctly on segments 11 and 1—3. Ocelli repeated as irregular black spots above and below the subdorsal line on segments 6—11 ; a small light spot near the posterior border of segments 5—10 (dorsal spots) and higher than the subdorsal line. Larva adult.

Figs. 24—28. Development of the markings of *Chærocampa Porcellus*.

Fig. 24. Stage I. ; immediately after emergence from the egg. Length, 3.5 millim.

Fig. 25. Stage II. ; after first moult. Length, 10 millim.

Fig. 26. Stage III. ; after second moult. Length, 2.6 centim.

Fig. 27. Eye-spots at this last stage ; subdorsal much faded, especially on segment 4. Position the same as in last Fig. ; magnified.

Fig. 28. Stage IV. ; after third moult ; corresponds exactly with Stage VI. of *C. Elpenor*. Dorsal view, with front segments partly retracted (attitude of alarm). Ocelli on segment 5 less developed than in *Elpenor* ; repetitions of ocelli as diffused black spots on all the following segments to the 11th ; two light spots on each segment from the 5th to the 11th, exactly as in *Elpenor* ; subdorsal line visible only on segments 1—3. Length, 4.3 centim.

Fig. 29. *Chærocampa Syriaca*. From a blown specimen in Lederer's collection, now in the possession of Dr. Staudinger. Length, 5.3 centim.

Fig. 30. First rudiments of the eye-spots of *Charocampa Elpenor*, Stage II. (corresponding also with Fig. 19 in position, the head of the caterpillar being to the left). Subdorsal line slightly curved on segments 4 and 5.

Fig. 31. Eye-spots at Stage III. of the larva Fig. 20 somewhat further developed (larva immediately before third moult). Position as in Fig. 20.

Fig. 32. Eye-spots at Stage IV corresponding to Fig. 21, A being the eye-spot of the fourth and B that of the fifth segment.

Fig. 33. Eye-spot at Stage V. of the larva of *C. Elpenor*; fourth segment.

Figs. 30—33 are free-hand drawings from magnified specimens.

Fig. 34. *Darapsa Chærilus* from N. America. Adult larva with front segments retracted. Copied from Abbot and Smith.

Fig. 35. *Charocampa Tersa*, from N. America. Adult larva copied from Abbot and Smith.

#### PLATE V.

Fig. 36. Sixth segment of adult *Papilio*-larvæ; A, *P. Hospiton*, Corsica; B, *P. Alexanor*, South France; C, *P. Machaon*, Germany; D, *P. Zolicaon*, California.

Figs. 37—44. Development of the markings of *Deilephila Euphorbiæ*.

Fig. 37. Stage I.; young caterpillar shortly after emergence. Natural length, 5 millim.

Fig. 38. Similar to the last, more strongly magnified. Natural length, 4 millim.

Fig. 39. Stage II.; larva immediately after first moult. The row of spots distinctly connected by a light stripe (residue of the subdorsal line). Natural length, 17 millim.

Fig. 40. Stage III.; after second moult; magnified

drawing of the last five segments. Only one row of large white spots on a black ground (ring-spots) ; subdorsal completely vanished ; the shagreen-dots formerly absent now appear in vertical rows interrupted only by the ring-spots. Below the latter are some enlarged shagreen-dots which subsequently become the second ring-spots. Natural length of the entire caterpillar, 21 millim.

Fig. 41. Stage IV. ; the same larva after the third moult. Transformation of the ground-colour from green to black, owing to the spread of the black patches proceeding from the ring-spots in Fig. 40 in such a manner as to leave between them only a narrow green triangle. The shagreen dots below the ring-spots have increased in size, but have not yet coalesced.

Fig. 42. Stage III. ; larva, same age as Fig. 40, but with *two rows* of ring-spots. Natural length of the whole caterpillar, 32 millim.

Fig. 43. Stage V. ; larva from Kaiserstuhl. Variety with only one row of ring-spots, and with red nuclei in the mirror-spots. Natural length, 5 centim.

Fig. 44. Stage V. ; larva from Kaiserstuhl (like the three preceding). The green triangles on the posterior edges of the segments in Fig. 42 have become changed into red. Natural length, 7.5 centim.

Fig. 45. *Deilephila Galii* ; Stage IV. Subdorsal with open ring-spots. Natural length, 3.4 centim.

Fig. 46. *D. Galii* ; adult larva ; Stage V. Brown variety with feeble shagreening ; subdorsal completely vanished. Natural length, 6 centim.

#### PLATE VI.

Fig. 47. The same species at the same stage. Black variety strongly shagreened ; similar to *Deil. Euphorbiæ*.



Fig. 48. Similar to the last. Yellow var. without any trace of shagreening.

Fig. 49. *Deilephila Vespertilio*. Three stages in the life of the species, representing three phyletic stages of the genus. A, life-stage III.=phyletic stage 3 (subdorsal with open ring-spots); B, life-stage IV.=phyletic stage 4 (subdorsal with closed ring-spots); C, life-stage V.=phyletic stage 5 (subdorsal vanished, only *one* row of ring-spots).

Fig. 50. *Deilephila Zygophylli*, from S. Russia; stage V. From a blown specimen in Staudinger's collection. In this specimen the ring-spots are difficult to distinguish on account of the extremely dark ground-colour; they are nevertheless present, and would probably be more distinct in the living insect. A, open ring-spot from another specimen of this species in the same collection.

Fig. 51. *Deilephila Nicæa*, from South France; Stage V. Copied from Duponchel.

Fig. 52. *Sphinx Convolvuli*; Stage V., segments 10—8. Brown variety, with distinct white spots at the points of intercrossing of the vanished subdorsal with the oblique stripes.

Fig. 53. *Anceyrx Pinastri*; A and B, larvæ immediately after hatching. Natural length, 6 millim.

Fig. 54. Same species; Stage II. Subdorsal, supra- and infra-spiracular lines developed. Natural length, 15 millim.

Fig. 55. *Smerinthus Populi*; Stage I. Immediately after hatching; free from all marking. Length, 6 millim.

Fig. 56. Same species at the end of first stage; lateral aspect. Length, 1.3 centim.

Fig. 57. Same species; Stage II. Subdorsal indistinct; the first and last oblique stripes more pronounced than the others. Length, 1.4 centim.

Fig. 58. *Deilephila Hippophaës* ; Stage III. Subdorsal with open ring-spot on the 11th segment. A, segment 11 somewhat enlarged. Length, 3 centim.

## PLATE VII.

Fig. 59. *Deilephila Hippophaës* ; Stage V. Secondary ring-spots on six segments (10—5).

Fig. 60. Same species ; Stage V. One or two red shagreen dots on segments 10—4 in the position of the ring-spots of Fig. 59. Length, 6.5 centim.

Fig. 61. Same species ; Stage V. Segments 9—6 of another specimen, more strongly magnified. A ring-spot on segments 9 and 8 showing its origin from two shagreen-dots ; two red shagreen-dots on segment 7, on segment 6 only one.

Fig. 62. *Deilephila Livornica* (Europe) in the last stage. Green form. Copied from Boisduval.

Fig. 63. *Pterogon Enotheræ* ; Stage IV. Length, 3.7 centim.

Fig. 64. The same species at the same stage ; dorsal view of the last segment.

Fig. 65. The same segment in Stage V. Eye-spot completely developed.

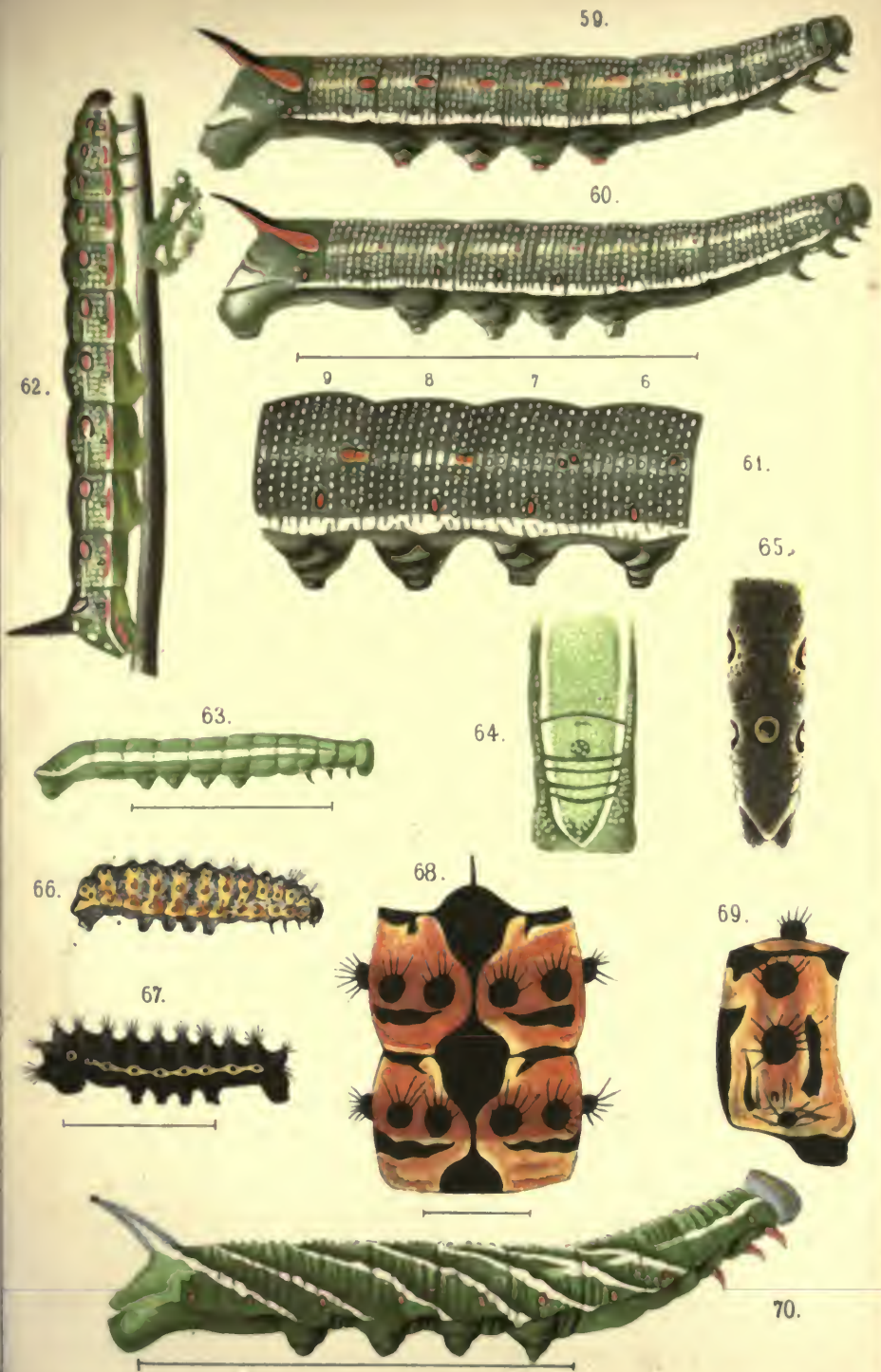
Fig. 66. *Saturnia Carpini*, larva from Freiburg ; Stage III. Natural length, 15 millim.

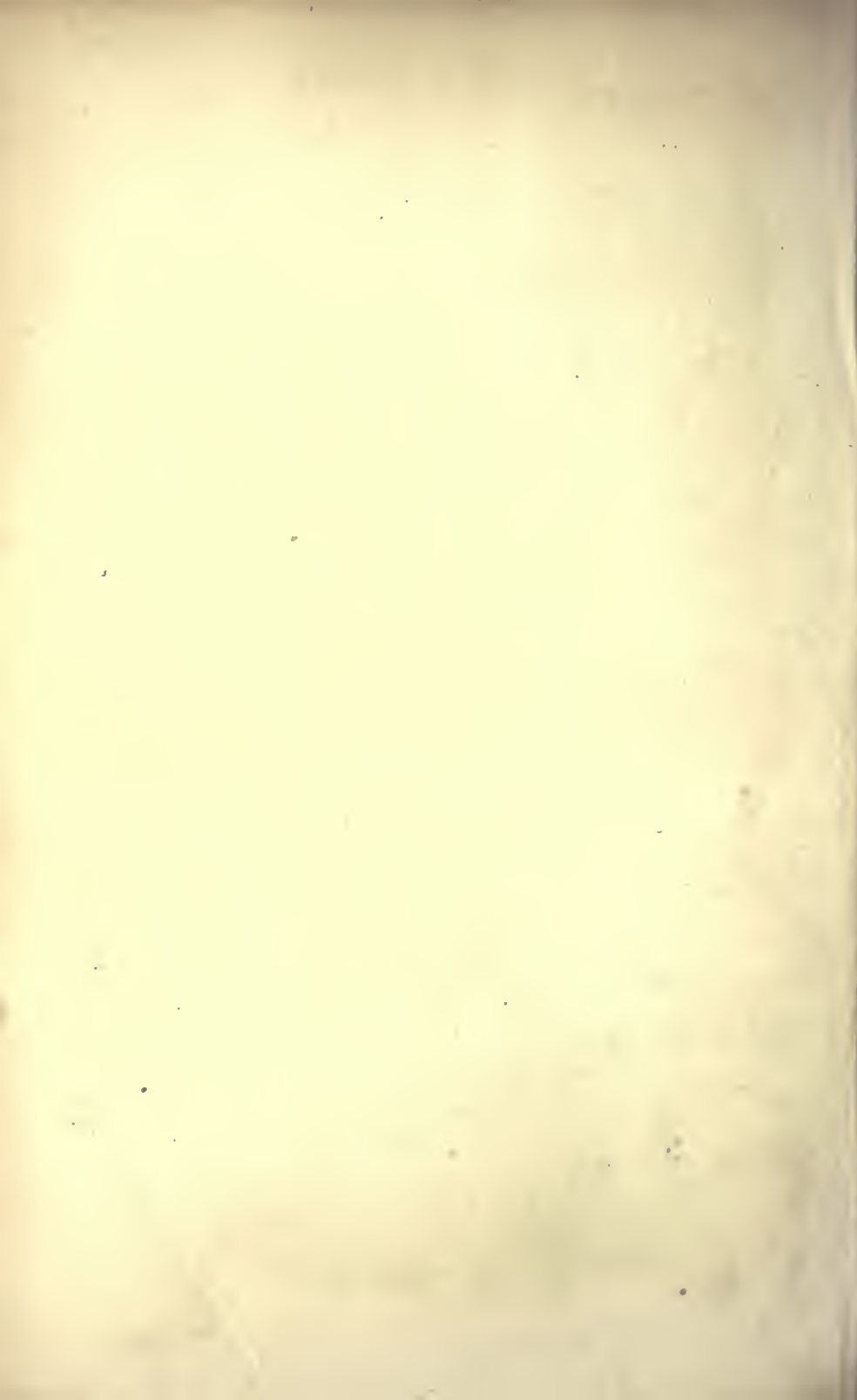
Fig. 67. Same species ; larva from Genoa ; Stage IV. Length, 20 millim.

Fig. 68. Same species ; larva from Freiburg ; Stage III. Segments 8 and 9 in dorsal aspect. Length, 15 millim.

Fig. 69. The same caterpillar ; lateral view of segment 8.

Fig. 70. *Smerinthus Ocellatus* ; adult larva with distinct subdorsal on the six foremost segments. The shagreening is only shown in the contour, elsewhere omitted. Length, 7 centim.



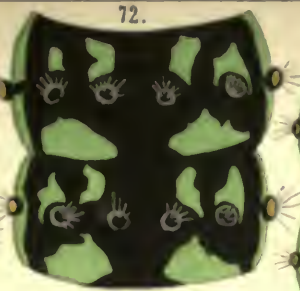




71.



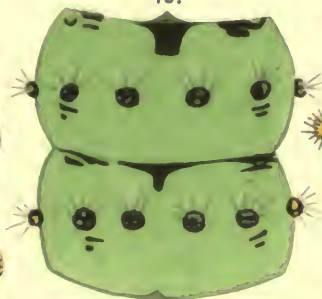
72.



73.



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74.



76.



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79.



78.



80.



81.



82.



83.



84.



85.



86.





PLATE VIII.

Figs. 71—75 represent segments 8 and 9 of the larva of *Saturnia Carpini* (German form) in dorsal aspect, all at the fourth stage. The head of the caterpillar is supposed to be above, so that the top segment is the eighth.

Fig. 71. *Saturnia Carpini*. Darkest variety.

Fig. 72. Lighter variety.

Fig. 73. Still lighter variety.

Fig. 74. One of the lightest varieties; the black extends further on segments 9 and 10 than on the 8th.

Fig. 75. Lightest variety.

Figs. 76—80 are only represented on a smaller scale than the remaining Figs. in order to save space; were they enlarged to the same scale they would be larger than the other figures.

Fig. 76. *Saturnia Carpini* (Ligurian form); Segment 8; Stage V.

Fig. 77. Same form; same segment in stage VI.

Figs. 78, 79, and 80. *Saturnia Carpini* (German form); dorsal aspect of 8th segment in Stage V. (the last of this form).

Fig. 78. Darkest variety.

Fig. 79. Lighter variety.

Fig. 80. Lightest variety.

Figs. 81—86. *Saturnia Carpini* (German form); Stage IV. Side view of the 8th segment in six different varieties. Fig. 81 shows only two small green spots at the bases of the upper warts besides the green spiracular stripes. Fig. 82 shows the spots enlarged and increased by a third behind the warts; the pro-legs have also become green.

Fig. 83. Two of the three green spots, which have become still more enlarged, are coalescent.

Fig. 84. All three spots coalescent ; but here, as also in

Fig. 85, various residues of the original black colour are left as boundary-marks.

Fig. 86. Lightest variety.

END OF PART II.



# STUDIES IN THE THEORY OF DESCENT.

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## Part III.

### ON THE FINAL CAUSES OF TRANSFORMATION.

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#### III.

##### THE TRANSFORMATION OF THE MEXICAN AXOLOTL INTO AMBLYSTOMA.

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###### INTRODUCTION.

SINCE the time when Duméril made known the transformation of a number of Axolotls into the so-called Amblystoma form, this Mexican Amphibian has been bred in many European aquaria, chiefly with the view to establish the conditions under which this transformation occurred, so as to be enabled to draw further conclusions as to the true causes of this exceptional and enigmatical metamorphosis.

Although the Amphibians propagated freely, the cases in which transformation occurred remained extremely rare, and it was not once

possible to reply to the main question, viz. whether this metamorphosis was determined by external conditions or by purely internal causes; to say nothing of the possibility of there perhaps being discoverable certain definite external influences by means of which the metamorphosis could have been induced with certainty. But while these points are undecided all attempted theoretical interpretations of the phenomenon must be devoid of a solid basis.

It appeared to me from the first that the history of this transformation of the Axolotl was of special theoretical value; indeed I believed that it might possibly furnish a special case for deciding the truth of those ground-principles, according to which the origin of this species is represented by the two conflicting schools as a case of transformation or as one of heterogenesis. I therefore determined to make some experiments with the Axolotl myself, in the hopes of being fortunate enough to be able to throw some light upon the subject.

In the year 1872 Prof. v. Kölliker was so good as to leave with me five specimens of his Axolotls, bred in Würzburg, and these furnished a numerous progeny in the following year. With these I carried out the idea, the theoretical bearing of which will be shown subsequently, whether it would not be possible to force all the larvæ, or at any rate, the greater majority, to undergo

transformation by exposing them to conditions of life which made the use of gills difficult, and that of lungs more easy; in other words, by compelling them to live partly on land at a certain stage of life.

During that year indeed I obtained no results, most of the larvæ perishing before the time for such an experiment had arrived, and the few survivors did not undergo transformation, but lived on to the following spring and then also died one after the other. Through long absence from Freiburg, necessitated by other labours, I had evidently left them without sufficient care and attention. I was thus led to the conviction, which was more fully confirmed subsequently, that no results can be obtained without the greatest care and attention in rearing, towards which single object all one's interest should be concentrated, and it must not be considered irksome to have to devote daily for many months a large amount of time to this experiment. As it was evident that I could not afford this time without calling in other aid, I hailed with pleasure an opportunity of witnessing the experiment performed by other hands.

A lady living here (Freiburg), Fräulein v. Chauvin, undertook to rear a number of my larvæ of the following year which had just hatched, and in accordance with my idea to make the experiment of forcibly compelling them to adopt the

Amblystoma form. How completely this was accomplished will be seen from the following notes by the lady herself, and it will no less appear that these results were only obtained by that care in treatment and delicacy of observation which she devoted to the experiments.

#### EXPERIMENTS.

“ I began the experiments on June 12th, 1874, with five larvæ about eight days old, these being the only survivors out of twelve. Owing to the extraordinary delicacy of these creatures, the quality and temperature of the water, and the nature and quantity of their food exerts the greatest influence, especially in early life, and one cannot be too cautious in their treatment.

“ The specimens were kept in a glass globe of about thirty centimeters in diameter, the temperature of the water being regulated ; as food at first Daphnids, and afterwards larger aquatic animals were introduced in large numbers. By this means all the five larvæ thrive excellently. At the end of June the rudiments of the front legs appeared in the most vigorous specimens, and on the 9th of July the hind legs also became visible. At the end of November I noticed that one Axolotl remained constantly at the surface of the water, and this led me to suppose that the right period had now arrived for effecting the



transformation into Amblystoma. For brevity I shall designate this as No. I., and the succeeding specimens by corresponding Roman numerals.

"In order to bring about this metamorphosis, on December 1st, 1874, No. I. was placed in a large-sized glass vessel containing earth arranged in such a manner that, when the vessel was filled with water, only one portion of the surface of the earth was entirely covered by the liquid, and the creature in the course of its frequent perigrinations was thus more or less exposed to the air. The water was gradually diminished on the following days, during which period the first changes made their appearance in the Amphibian—the gills commenced to shrivel up, and at the same time the creature showed a tendency to seek the shallowest spots. On December 4th, it took entirely to the land, and concealed itself among some damp moss which I had placed on a heap of sand on the highest portion of the earth in the glass vessel. At this period the first ecdysis occurred. Within the four days from the 1st to the 4th of December, a striking change took place in the external appearance of No. I., the gill-tufts shrivelled up almost entirely, the dorsal crest completely disappeared, and the tail, which had hitherto been broad, became rounded and similarly formed to that of a land salamander. The grey-brown colour of the body changed gradually into a blackish hue; isolated spots, at first

of a dull white, made their appearance and these in time increased in intensity.

“When the Axolotl left the water on December 4th the gill-clefts were still open, but these closed gradually, and after about eight days were overgrown with skin and no longer to be seen.

“Of the other larvæ three appeared at the end of November (*i.e.* at the same time when No. I. came to the surface of the water) to have kept pace in development with No. I., an indication that for these also the right period had arrived for accelerating the developmental processes. They were therefore submitted to the same treatment as No. I. No. II. became transformed at the same time and exactly in the same manner as the latter; its gill-tufts were complete when it was first placed in the shallow water, but after four days these had almost entirely disappeared; in the course of about ten days after it took to the land, the overgrowth of skin on the gill-clefts and the complete assumption of the salamander form occurred. During this last period the creature took food, but only when urged to do so.

“In Nos. III. and IV. the development proceeded more slowly. Neither of these so frequently sought the shallow spots, nor did they as a rule remain so long exposed to the air, so that the greater part of January had expired before they took entirely to the land. Nevertheless the dessication of the gill-tufts did not take a longer time

than in Nos. I. and II. as the first ecdysis occurred as soon as they took to the land.

" No. V. showed still more striking deviations in its transformation than Nos. III. and IV., but as this specimen appeared much weaker than the others from the beginning and was retarded in growth to a most notable extent, this is by no means surprising. It took fourteen instead of four days before the transformation had advanced far enough to enable it to leave the water. It was especially interesting to observe the behaviour of this specimen during this period. Its weak and delicate constitution evidently made it much more susceptible to all external influences than the others. If exposed to the air for too long a time it acquired a light colour, and when annoyed or alarmed it emitted a peculiar odour, similar to that of a salamander. As soon as these phenomena were observed it was at once placed in deeper water, into which it immediately plunged and gradually recovered itself, the gills always becoming again expanded. The same experiment was repeated several times and always led to the same result, from which we may venture to conclude that by accelerating the transformation too energetically, the process may come to a standstill, and even by continued compulsion may end in death.

" It yet remains to be mentioned with respect to Axolotl No. V. that this specimen, unlike all the

others, did not emerge from the water at the first ecdysis, but at the time of the fourth.

"All the Axolotls are now (July, 1875) living, and are healthy and vigorous, so that with respect to their state of nourishment there is nothing to prevent their propagating. Of the first four the largest is fifteen centim. long; Axolotl No. V. measures twelve centim.

"The preceding statements appear to demonstrate the correctness of the views advanced in the Introduction:—Axolotl larvæ generally but not always complete their metamorphosis if, in the first place, they emerge sound from the egg and are properly fed; and if, in the next place, they are submitted to the necessary treatment for changing aquatic into aërial respiration. It is obvious that this treatment must only be applied very gradually, and in such a manner as not to overtax the vital energy of the Amphibian."

To the foregoing remarks of Fräulein v. Chauvin I may add that in all five cases the transformation was complete, and not to be confounded with that change which occurs more or less in all Axolotls in the course of time when confined in small glass vessels. In this last case there frequently appear changes in the direction of the Amblystoma form without the latter being actually reached. In the five adult Axolotls which I possessed for a short time, and of which two were at least four years old,



the gills were much shrivelled, but the aquatic tail and dorsal crest were unchanged. The crest may, however, also disappear, and the tail become shortened without these changes being due to a transformation into *Amblystoma*, as will be shown further on.

With respect to the duration of the transformation, this amounted in Axolotls Nos. I. to IV. altogether to twelve or fourteen days. Of these, four days were taken by the first changes which occurred while the creature was still in the water; the remaining time, to the completion of the metamorphosis, was passed on land. Duméril gives the duration of the metamorphosis as sixteen days.

The following results of the experiments just described appear to me to be especially noteworthy:—The five Axolotl larvæ which can alone be taken into consideration, the others having soon perished, all experienced metamorphosis, and without an exception became *Amblystomas*. Only one of them, No. I., by persistently swimming at the surface, as was observed at the end of six months, showed a decided tendency to undergo metamorphosis and to adopt aerial respiration. With respect to this specimen it may therefore be confidently assumed that it would have taken to the land, and that metamorphosis would have occurred without artificial aid, just as was the case in the thirty specimens which Duméril altogether observed.

Respecting Nos. II., III., and IV., on the other hand, such a supposition is but little probable. These three larvæ endeavoured to keep in deep water and avoided as long as possible the shallow places which would have enforced them to take entirely to lung breathing. Metamorphosis thus occurred more than a month later in these individuals.

Finally, there can scarcely be any doubt that No. V. would not have become transformed without forcible adaptation to an aërial life.

From these results we may venture to conclude that most Axolotl larvæ change into the Amblystoma form when, at the age of six to nine months, they are placed in such shallow water that they are compelled to respire chiefly by their lungs. The experiments before us are certainly at present but very few in number, but such a conclusion cannot be termed premature if we consider that out of several hundred Axolotls (the exact number is not given) Duméril obtained only about thirty Amblystomas, while v. Köl liker bred only one Amblystoma out of a hundred Axolotls.

It now only remains questionable whether *each larva* could have been forced to undergo metamorphosis, but this could only be decided by new experiments. It was originally my intention to have delayed the publication of the experiments till Fräulein v. Chauvin had repeated them in larger numbers, but as my Axolotls have not bred this

year (1875) I must abandon my scheme, and this can be done the more readily because, for the theoretical consideration of the facts, it is immaterial whether *all* or only *nearly all* the Axolotls could have been compelled to undergo transformation. I must not, however, omit to mention that Herr Gehrig, the curator of our Zoological Museum, bred a considerable number of larvæ from the same brood as that with which Fräulein v. Chauvin experimented, and that of these larvæ six lived over the winter *without undergoing metamorphosis*. They were always kept in deep water and thus furnished the converse experiment to those recorded above; they further prove that this whole brood did not have a previous tendency to undergo metamorphosis.

If these new facts are to be made use of to explain the nature of this extraordinary process of transformation in accordance with our present conception, the data already known must in the first place be called to our aid.

It has first to be established that *Siredon Mexicanus* never, as far as we know, undergoes metamorphosis in its native country. This Amphibian is there only known in the *Siredon* form, a statement which I have taken from De Saussure,<sup>1</sup> who has himself observed the Axolotl in the Mexican lakes. This naturalist never found a single

<sup>1</sup> Verhandl. Schweiz. Naturforsch. Gesellschaft. Einsiedeln, 1868.

Amblystoma in the neighbourhood of the lakes, "nevertheless the larva (Axolotl) is so common there that it is brought into the market by thousands." De Saussure believes that in Mexico the Axolotl does not undergo transformation.<sup>2</sup> The same statement is distinctly made by Cope,<sup>3</sup> whose specimens of *Siredon Mexicanus* bred in America, even in captivity showed "no tendency to become metamorphosed." On the other hand Tegetmeier observed<sup>4</sup> that one out of five specimens obtained from the Lake of Mexico underwent metamorphosis, and this accordingly establishes the second fact, viz. that the true Axolotl becomes transformed under certain conditions into an Amblystoma when in captivity.

This last remark would be superfluous if, as was for a long time believed, the Paris Axolotls, of which the metamorphosis was first observed and which at the time made such a sensation, were actually *Siredon Mexicanus*, i.e. the *Siredon* which alone in its native country bears the name of Axolotl. In his first communication Duméril was himself of this opinion; he then termed the animal

<sup>2</sup> [Eng. ed. In 1878 Señor José M. Velasco published a paper entitled "Descripción, metamorfosis, y costumbres de una especie nueva del género *Siredon*." Memor. Sociedad Mexicana de Historia Natural, December 26th. See Addendum to this essay].

<sup>3</sup> Dana and Silliman's Amer. Journ., 3rd series, i. p. 89. Annals Nat. Hist. vii. p. 246.

<sup>4</sup> Proc. Zoo. Soc. 1870, p. 160.



"*Siredon Mexicanus vel Humboldtii*,"<sup>5</sup> but subsequently, in his amplified work<sup>6</sup> on the transformation of the Axolotl observed in the Jardin des Plantes, he retracted this view, and after a critical comparison of the five described species of *Siredon*, he came to the conclusion that the species in the possession of the Paris Museum was probably *Siredon Lichenoides* (Baird). All the transformations of Axolotls observed in Europe must consequently be referred to this species, since they were—at least as far as I know—all derived from the Paris colony. My own experimental specimens were also indirectly descended from these.

Now it must be admitted that this does not coincide with the fact that the *Amblystoma* form which Duméril first obtained from his Axolotls agreed with Cope's species, *A. Tigrinum*, while on the other hand we learn from Marsh<sup>7</sup> that *Siredon Lichenoides* (Baird), when it does undergo metamorphosis, becomes transformed into *Amblystoma Mavortium* (Baird).

Marsh found *Siredon Lichenoides* in mountain lakes (7000 feet above the sea) in the south-

<sup>5</sup> Compt. Rend., vol. lx. p. 765 (1865).

<sup>6</sup> Nouvelles Archives du Muséum d'Histoire Nat. Paris, 1866, vol. ii. p. 268.

<sup>7</sup> Proc. Boston Soc., vol. xii. p. 97; Silliman's Amer. Journ., vol. xlv. p. 364; reference given in "Troschel's Jahresbericht" for 1868, p. 37.

west of the United States (Wyoming Territory), and obtained from them, by breeding in aquaria, *Amblystoma Mavortium* (Baird). He considers it indeed doubtful whether the Amphibian undergoes this transformation in its native habitat, although he certainly states this opinion without rigorous proof on purely theoretical considerations, because, according to his view, "the low temperature is there less favourable."<sup>8</sup>

If I throw doubt upon this last statement it is simply because *Amblystoma Mavortium* is found native in many parts of the United States, viz :— in California, New Mexico, Texas, Kansas, Nebraska, and Minnesota. It is indeed by no means inconceivable that in the mountain lakes where Marsh obtained this species, it may behave differently with respect to metamorphosis than in other habitats, and this appears probable from certain observations upon *Triton* which will be subsequently referred to.

Meanwhile, in the absence of further observations, we must admit that the Paris Axolotls were not *Siredon Lichenoides*, but some nearly allied and probably new species. But little information is furnished by observing the course of the transformation, although it is at least established that this

<sup>8</sup> Proc. Boston Soc., vol. xii. p. 97 ; Silliman's Amer. Journ., vol. xlvi. p. 364. I have not been able to get a copy of this paper, and quote from a reference in "Troschel's Jahresbericht." See preceding note.

Axolotl in its native habitat does not undergo metamorphosis or does so as exceptionally as in Europe. Unfortunately in his papers Duméril gives no precise statement respecting the locality of this species imported from "Mexico"—it is probable that he was himself unacquainted with it, so that I can only state on the authority of Cope that *Amblystoma* has never been brought from south of the provinces of Tamaulipas and Chilhuahua, *i. e.* south of the Tropic of Cancer.<sup>9</sup>

This last statement, however, gives no certainty to the matter. Of much more importance is the above-mentioned fact, that the true Axolotl of the lakes about the city of Mexico does not, as a rule, become transformed into an *Amblystoma* in that locality, although this species in certain cases undergoes metamorphosis when in confinement. From this circumstance and from the fact that the Paris Axolotl likewise experienced but a very small percentage of metamorphosis in captivity, we may venture to conclude that this species also, in its native habitat, either does not become transformed at all or does so only exceptionally.

But there is yet another body of facts which come prominently into view on considering the history of the transformations. I refer to the existence of numerous species of *Amblystoma* in a natural state. In the "Revision of the genera of

<sup>9</sup> Dana and Silliman's Amer. Journ. See note 3.

*Salamandridæ*," published some years ago by Strauch,<sup>10</sup> this author, following Cope,<sup>11</sup> gives twenty species of *Amblystoma* as inhabiting North America. Although some of these species are based on single examples, and consequently, as Strauch justly remarks, "may well have to be reduced in the course of time," there must nevertheless always remain a large number of species which live and propagate as true *Amblystomas*, and of which the habitat extends from the latitude of New York to that of New Mexico. There are therefore true species of *Siredon* which regularly assume the *Amblystoma* form under their natural conditions of life, and which propagate in this form, while, on the other hand, there are at least two species which, under their existing natural conditions of life, always propagate as *Siredon*. It is but another mode of expression for the same facts if we say that the Mexican Axolotl and the Paris *Siredon*—whether this is *Lichenoides* or some other species—stand at a lower grade of phyletic development than those species of *Amblystoma* which propagate in the salamander form. No one can raise any objection to this statement, while the alternative view maintained by all authors contains a theory either expressed or implied which is, as I believe, incorrect, viz. that the Mexican Axolotl

<sup>10</sup> Proc. Acad. Philadelph. xix. 1867, pp. 166—209.

<sup>11</sup> Mém. Acad. Petersb. vol. xvi.



*has remained* at an inferior stage of phyletic development.

All zoologists<sup>12</sup> who have expressed an opinion upon the transformation of the Axolotl, and who are not, like the first observer of this fact, embarrassed by Cuvier's views as to the immutability of species, regard the phenomenon as though a species, which owing to some special conditions had hitherto remained at a low stage of development, had now through some other influences been compelled to advance to a higher stage.

I believed for a long time that the phenomenon could not otherwise be comprehended, so little was I then in a position to bring all the facts into harmony with this view. Thus in the year 1872 I expressed myself as follows<sup>13</sup>:—"Why should not a sudden change in all the conditions of life (transference from Mexico to Paris) have a direct action on the organization of the Axolotl, causing it suddenly to reach a higher stage of development, such as many of its allies have already attained, and which obviously lies in the nature of its organization—a stage which it would perhaps itself have

<sup>12</sup> [Eng. ed. Seidlitz is an exception, since in his work on Parthenogenesis (Leipzig, 1872, p. 13) he states that "In the Axolotl, Pædogenesis, which is not in this case . . . monogamous, but sexual, and indeed gynækogenetic, has already become so far constant that it has perhaps entirely superseded the orthogenetic reproduction."]

<sup>13</sup> Über den Einfluss der Isolirung auf die Artbildung. Leipzig, 1872, p. 33.

reached, although later, in its native country? Or is it inconceivable that the sudden removal from 8000 feet above the sea (Mexican plateau) to the altitude of Paris, may have given the respiratory organs an impetus in the direction of the transformation imminent? In all probability we have here to do with the direct action of changed conditions of life."

That the substance of this last statement must still hold good is obvious from the experiments previously described, which show that by the application of definite external influences, we have it to a certain extent in our power to produce the transformation. It is precisely in this last point that there lies the new feature furnished by these experiments.

But are we also compelled to interpret the phenomenon in the above manner? *i. e.* as a sudden advance in the phyletic development of the species occurring, so to speak, at one stroke? I believe not.

What first made this view appear to me erroneous, was the appearance of the living *Amblystomas* bred from my *Axolotl* larvæ. These creatures by no means differed from the *Axolotls* merely in single characters, but they were distinct from the latter in their entire aspect; they differed in some measure in all their parts, in some but slightly and in other parts strongly—in brief, they had become quite different animals. In accord-

ance with this, their mode of life had become completely modified ; they no longer lived in the water, but remained concealed by day among the damp moss of the vivarium, coming forth only by night in search of food in dry places.

I had been able to perceive the great difference between the two stages of development from the anatomical data with which I had long been familiar, and which Duméril had made known with respect to the structure of his Amblystomas. But the collecting of numerous details gives no very vivid picture of the metamorphosis ; it was the appearance of the living animal that first made me conscious how deep-seated was the transformation which we have here before us, and that this change not merely affected those parts which would be directly influenced by the change in the conditions of life, such as the gills, but that most if not all the parts of the animal underwent a transformation, which could in part be well explained as morphological adaptation to new conditions of life, and partly as a consequence of this adaptation (correlative changes), but could not possibly be regarded as the sudden action of these changed conditions.

Such at least is my view of the case, according to which a *per saltum* development of the species of such a kind as must here have taken place, is quite inconceivable.

I may venture to assume that most observers

of the metamorphosis of Axolotl have, like myself, not been hitherto aware of the extent of the transformation, and it may thus be explained why the theoretical bearings of the case have on all sides been incorrectly conceived. We have here obviously a quite extraordinary case of the first order of importance. I believe that it can easily be shown that the explanation of the history of the metamorphosis of the Paris Axolotl which has hitherto been pretty generally accepted, necessarily comprises a very far-reaching principle. If this interpretation is correct, then in my opinion must also hold good the ideas of those who, like K  lliker, Askenasy, N  geli, and, among the philosophers, Hartmann and Huber, would refer the transformation of species in the first instance to a power innate in the organism, to an active, *i.e.* a self-urging "law of development"—a phyletic vital force.

Thus, if the Axolotls transformed into Amblystomas are regarded as individuals which, impelled by external influences, have anticipated the phyletic development of the others, then this advance can only be ascribed to a phyletic vital force, since the transformation is sudden, and leaves no time for gradual adaptation in the course of generations. The *indirect* influence of the external conditions of life, *i. e.* natural selection, is thus excluded from the beginning. But the *direct* action of the changed conditions of life by no means furnishes



an explanation of the complete transformation of the whole structure, such as I have already alluded to, and which I will now enter into more closely.

The differences between the Paris Axolotl and its *Amblystoma* according to Duméril, Kölliker, and my own observations are as follow :—

1. The gills disappear ; the gill-clefts close up, and of the branchial arches only the foremost remain, the posterior ones disappearing. At the same time the *os hyoideum* becomes changed (Duméril).

2. The dorsal crest completely disappears (Duméril).

3. The aquatic tail becomes transformed into one like that of the salamanders (Duméril), which, however, is not as in the salamander cylindrical, but somewhat compressed laterally (Weismann).

4. The skin becomes yellowish white, irregularly spotted on the sides and back (Duméril), whilst at the same time its former grey-black ground-colour changes into a shining greenish black (Weismann) ; it loses, moreover, the slimy secretion of the skin, and the cutaneous glands become insignificant (Kölliker).

5. The eyes become prominent and the pupils narrow (Kölliker), and eye-lids capable of completely covering the eyes are formed ; in Axolotl only a narrow annular fold surrounds the eyes, so that these cannot be closed (Weismann).

6. The toes become narrowed and lose their

skin-like appendages (Köl liker), or more precisely, the half webs which connect the proximal extremities of the toes on all the feet (Weismann).

7. The teeth are disposed in this species, as in all other *Amblystomæ*, in transverse series ; whilst in Axolotl, as in *Triton* larvæ, they are arranged at the sides of the jaw in the form of a curved arch-like band beset with several rows of teeth.<sup>14</sup> (Duméril. See his fig., *loc. cit.* p. 279).

8. In Axolotl the lower jaw, in addition to the teeth on the upper edge of the bone, also bears "de très petites dents disposées sur plusieurs rangs ;" these last disappear after metamorphosis (Duméril). I will add that the persistent teeth belong to the *os dentale* of the lower jaw, and those that are shed to the *os operculare*.<sup>15</sup>

9. The surface of the posterior moveable part of the body is slightly concave both before and after transformation ; the anterior part is, how-

<sup>14</sup> Duméril represents the teeth of the *vomer* as separated from those of the *os palatinum* by a gap. This is probably accidental, since Gegenbaur (Friedrich u. Gegenbaur, the skull of Axolotl, Würzburg, 1849) figures the rows of teeth as passing over from the one bone to the other without interruption. This was the case with the Axolotls which I have been able to examine on this point ; but this small discrepancy is, however, quite immaterial to the question here under consideration.

<sup>15</sup> See O. Hertwig "Über das Zahnsystem der Amphibien und seine Bedeutung für die Genese des Skelets der Mundhöhle." Archiv. für microsc. Anat., vol. xi. Supplement, 1874.

ever, less concave in *Amblystoma* than in *Siredon* (Duméril).

I have not yet been able to verify Duméril's 7th and 9th statements, as I did not want to kill any of my living *Amblystomas*,<sup>16</sup> simply in order to confirm the observations of a naturalist in whom one may certainly place complete confidence. Neither have I as yet observed the transformation of the branchial arches, but all the other statements of Köl liker and Duméril I can entirely corroborate.

The structural differences between Axolotl and *Amblystoma* are considerably greater and of more importance than those between allied genera, or indeed than between the families of the Urodela. The genus *Siredon* undoubtedly belongs to a different sub-order to the genus *Amblystoma* into which it occasionally becomes transformed. Strauch, the most recent systematic worker at this group, distinguishes the sub-order *Salaman-drida* from that of the *Ichthyodea* by the possession of eyelids, and by the situation of the palatine teeth in single rows on the posterior edge of the palatal bone: in *Ichthyodea* the eyelids are wanting and the palatine teeth are either "situated on the anterior edge of the palatal bone," or

<sup>16</sup> [Eng. ed. These *Amblystomas* have since died and have been minutely described by Dr. Wiedersheim. See his memoir, "Zur Anatomie des *Amblystoma Weismanni*," in *Zeit. für wiss. Zool.*, vol. xxxii. p. 216.]

"cover the whole surface of the palatal plates in brush-like tufts."

How is it possible to regard such widely divergent anatomical characters as changes suddenly produced by the action (but once exerted) of deviating conditions of life? Hand in hand with the shedding of the old and the appearance of new palatine teeth, there occurs a change in the anatomical structure of the vertebral column, and also—as we may fairly conclude from Kölliker's correct observation of the cessation of the slimy secretion—in the histological structure of the skin. Who would undertake to explain all these profound modifications as the direct and sudden action of certain external influences? And if any one were inclined to explain such changes as a consequence of the disappearance of the gills, *i.e.* as correlative changes, what else is such a correlation than the phyletic vital force under another name?

If from one change arising from the direct action of external agencies, the whole body can in two days become transformed in all its parts, in the precise manner which appears best adapted for the new conditions of life under which it is henceforward to exist, then the word "correlation" is only a phrase which explains nothing, but which prevents any attempt at a better explanation, and it would be preferable to profess simply the belief in a phyletic vital force.



Moreover, it is hardly permissible to seek such an explanation, since Urodela are known which have no gills in the adult state, and which nevertheless possess all the other characters of the *Ichthyodea*, viz. want of eyelids, characteristic palatine teeth, and the tongue bone. This is the case with the genera *Amphiuma* (Linn.), *Menopoma* (Harl.), and *Cryptobranchus* (v.d.Hoev.). The two first genera, as is known, still possess gill-clefts, but *Cryptobranchus* has even lost these clefts, which, as in *Amblystoma*, are overgrown by skin; nevertheless *Cryptobranchus* is, according to the concurrent testimony of all systematists, a true salamander in habits, tongue bone, palatine teeth,<sup>17</sup> &c. It must further be added that the Axolotl itself can lose the gills without thereby becoming transformed into an *Amblystoma*. I have previously mentioned that in Axolotls which were kept in shallow water the gills frequently became diminutive, and it also sometimes happens that they completely shrivel up. I possess an Axolotl preserved in alcohol in which the gills have shrivelled up into small irregular bunches, and the dorsal crest is also so completely absent that its place is occupied by a long furrow, and even on the tail the crest has entirely disappeared from the lower edge and about half from the upper edge. Notwithstanding this, the creature is widely removed from *Amblystoma* in structure; it possesses

<sup>17</sup> See Strauch, *loc. cit.* p. 10.

the arched branchial apparatus, the palatine teeth, the skin, &c., of the Axolotl.

These facts prove, therefore, that the shedding of the gills by no means always entails all the other modifications which we observe in the metamorphosis of Axolotl, so that these modifications are thus not by any means the necessary and immediate consequence of such gill shedding.

Whether these modifications will occur after a long series of generations—whether the successors of *Cryptobranchus* will also one day acquire the salamandriform structure is another question, and one which I could not exactly answer in the negative. But this question does not here come into consideration, as we are now only concerned with the *immediate result* of the shedding of the gills.

The problem appears therefore to be as follows:—Either the hitherto received interpretation of the transformational history of the Axolotl as a further development of the species is incorrect, or else the case of Axolotl incontestably proves the existence of a phyletic vital force.

We have now to ask whether the facts of this transformational history are not capable of another explanation.

I believe that this is certainly possible, and that another interpretation can be shown to be correct with some degree of probability.

I am of opinion that those Amblystomas which

have been developed in captivity in certain instances from *Siredon Mexicanus* (*S. Pisciformis*), as well as from the Paris Axolotls, are not progressive, but reversion forms; I believe that the Axolotls which now inhabit the Mexican lakes were Amblystomas at a former geological (or better, zoological) epoch, but that owing to changes in their conditions of life, they have reverted to the earlier perennibranchiate stage.

I was undoubtedly first led to this conception by the results which arose from my studies on the seasonal dimorphism of butterflies.<sup>18</sup> In this case we were also concerned with the two different forms under which one and the same species appears, and of which it was shown to be probable that the one is phyletically older than the other. The younger summer form, according to my view, has arisen, through the gradual amelioration of the climate, from the winter form, which at an earlier zoological epoch was the only one in existence; but the latter, the primary form, has not for this reason ceased to exist, but now alternates in each year as a winter form with the secondary summer form.

Now with seasonally dimorphic butterflies, it was easily possible to induce the summer brood to assume the winter form by exposing their pupæ for a long time to a low temperature; and it was shown to be highly probable that this abrupt and

<sup>18</sup> See Part I. of this volume.

often very extensive change or transformation, only apparently takes place suddenly, and is but the apparent result of the action of cold upon this generation, whilst in fact it depends upon reversion to the primary form of the species, so that the low temperature, which is only once applied, gives but the impetus to reversion, and is not the true cause of the transformation. This cause must rather be sought in the long continued action of the cold to which the ancestors of our existing butterflies were subjected for thousands of generations, and of which the final result is the winter form.

If we assume for an instant that my interpretation of the transformation of Axolotl as just offered is correct, we should have conditions in many respects analagous to those of seasonal dimorphism. It is true that in this case the two forms no longer alternate regularly with each other, but the primary form may occasionally appear instead of the secondary form, owing to the action of external conditions.

Just as in the case of seasonal dimorphism it is possible to compel the summer generation to abandon the summer form, and to assume the winter guise by the action of cold; so in the present case we are able to induce the Axolotl to adopt the *Amblystoma* form by making aërial respiration compulsory at a certain stage of life; and further, just as in seasonal dimorphism it can



be shown that this artificially produced change is only apparently an abrupt transformation, and is actually a reversion to the much older winter form; so here we have not an actual, but only an apparent remodelling of the species—a reversion to the phyletically older form.

This certainly appears a paradox, inasmuch as a form here arises by reversion which must yet undoubtedly rank as the more highly developed. I believe, however, that much which seems paradoxical in this statement will disappear on further examination.

It must in the first place be taken into consideration that the phyletic development of species need not by any means always take place by advancement. We have indeed many cases of retrogressive development, although in a somewhat different sense, as with parasites and those forms which have degenerated from free locomotion to a sedentary mode of life.<sup>19</sup> I do not confuse this kind of retrogressive development, arising from the arrest of certain organs and

<sup>19</sup> [This is the principle of "Dégénération" recognized by Darwin (see "Origin of Species," 6th ed. p. 389, and "Descent of Man," vol. i. p. 206), and given fuller expression to by Dr. Anton Dohrn (see his work entitled "Der Ursprung der Wirbelthiere und das Princip des Functionswechsels." Leipzig, 1875). A large number of cases have been brought together by Prof. E. R. Lankester, in his recent interesting work on "Degeneration, a Chapter in Darwinism." Nature series, 1880. R.M.]

systems of organs, with true reversion. The latter is a return to a form which has already been once in existence ; but in the former case, in spite of all simplification of the organization, some entirely new feature always comes into existence. But I am not able to see any absurdity in the assumption that even true reversion, whether of a whole species or of the individuals of a certain district, may be regarded as possible, and I require no further concession. Why, for example, should it be inconceivable that at a very remote period the Axolotl was adapted to a life on land ; that through the direct and indirect action of changed conditions of life it gradually acquired the salamander form, but that subsequently, through new and unfavourable changes in the conditions of life, it again relapsed to the older form, or at least to one nearly related thereto ?

At any rate such an assumption contains nothing opposed to known facts, but can be supported in many ways, and finally it commends itself, at least in my opinion, as offering the only admissible explanation of the facts before us.

The existence of a whole series of species of *Amblystoma*, as already mentioned, at once shows that species of *Siredon* can become elevated into the salamander form, and can propagate regularly in this state, and further, that this phyletic advance has already actually taken place in many species.

That degeneration may also occur from this high stage to a lower stage of development, is shown by many observations on our water-salamanders. It is known that under certain circumstances Tritons, as it is generally expressed, become "sexually mature in the larval condition."

In the year 1864 De Filippi<sup>20</sup> found fifty Tritons in a pool at Andermatten, in the neighbourhood of Puneigen, and of these only two showed the structure of the adult water-salamander; all the others still possessed gills, but notwithstanding this, they agreed in both sexes, in size and in the development of the sexual organs, with mature animals. De Filippi established that these "sexually mature larvæ" not only resembled larvæ externally through the possession of gills, but that they also possessed all the other anatomical characters of the larvæ, *i. e.* the characteristic bunches of palatine teeth situated on both sides in the position of the subsequent single rows, and a vertebral column represented throughout its whole length by the *chorda dorsalis*.

According to my view this would be a case of the reversion of the Triton to the immediately anterior phyletic stage, *i. e.* to the perennibranchiate stage, and in the present instance the majority of zoologists who take their stand by the theory of descent, would certainly concur in this view. I

<sup>20</sup> "Sulla Larva del *Triton Alpestris*." Archivio per la Zoologia. Genova e Torino, 1861, vol. i. pp. 206—211.

should at least consider it to be a useless play upon words did we here speak of larval reproduction, and thereby believe that we had explained something. The animal certainly becomes sexually mature in the same condition as that in which it first appears as a larva, but we first get an insight into the nature of this process by considering that this so-called "sexually mature larva" has the precise structure which must have been possessed by the preceding phyletic stage of the species, and that an individual reversion to the older phyletic stage of the species is consequently before us. I maintain that Duméril is in error in regarding this case of the Triton as parallel with the true larval reproduction of Wagner's *Cecidomyia* larva. In this last case it is certainly not reversion to an older phyletic stage that confers the power of reproduction upon the larvæ, since the latter do not represent an older phyletic stage of the species, but must have arisen contemporaneously with this last stage. The enormous structural difference between the larvæ and the imagines is not explained by the latter having arisen from the former supplementarily as a finished production, but by both having been contemporaneously adapted to continually diverging conditions of life.<sup>21</sup> Considered phyletically, these larvæ are by no means necessarily transitional to the origination

<sup>21</sup> See also Lubbock "On the Origin and Metamorphoses of Insects," London, 1874.



of the flies. They could have been quite different without the form of the imagines having been thereby modified, since the stages of insect metamorphosis vary independently of each other in accordance with the conditions of life to which they are subjected, and exert scarcely any, or only a very small form-determining influence upon each other, as has been amply proved in the preceding essay. In any case the power of these larvæ (the *Cecidomyiæ*) to propagate themselves asexually was first acquired as a secondary character, as appears from the fact that there exist numerous species of the same genus which do not "nurse." In the form which they now possess they could never have played the part of the final stage of the ontogeny, nor could they formerly have possessed the power of sexual reproduction.<sup>22</sup> In brief, we are here concerned with true larval reproduction, whilst in Triton we have reversion to an older phyletic stage.<sup>23</sup>

<sup>22</sup> See the first essay "On the Seasonal Dimorphism of Butterflies," p. 82.

<sup>23</sup> [Eng. ed. It has frequently been objected to me that the existing Axolotl is not a form resulting from atavism, but a case of "arrested growth." The expression "atavism" is certainly to be here taken in a somewhat different sense than, for example, in the case of the reversion of the existing Axolotl to the Amblystoma form. Further on, I have myself insisted that in the first case the phyletic stage in which the reversion occurred is still completely preserved in the ontogeny of each individual, whilst the Amblystoma stage has become lost in the ontogeny of the Axolotl. If, therefore, we apply the term "atavism" only to

I cannot agree with my friend Professor Haeckel when he occasionally designates the reversion of

such characters or stages (*i. e.* complexes of characters) as are no longer preserved in the ontogeny, we cannot thus designate the present arrest of the Axolotl at the perennibranchiate stage. Such a restriction of the word, however, appears to me but little desirable, since the process is identical in both cases, *i. e.* it depends upon the same law of heredity, in accordance with which a condition formerly occurring as a phyletic stage suddenly reappears through purely internal processes. It is true that the reversion is not *complete*, *i. e.* the present sexually mature Axolotl does not correspond in all details with its perennibranchiate ancestors. Since Wiedersheim has shown that the existing Axolotl possesses an intermaxillary gland, this can be safely asserted. This gland occurs only in *land* Amphibians, and therefore originated with the Amblystoma form, afterwards becoming transferred secondarily to the larval stage. Nevertheless, the present Axolotl must resemble its perennibranchiate ancestors in most other characters, and we should be the more entitled to speak of a reversion to the perennibranchiate stage as we speak also of the reversion of single characters. To this must be added that the Axolotl does not correspond exactly with an Amblystoma larva, since Wiedersheim has shown that the space for the intermaxillary gland is present, but that the gland itself is confined to a few tubes which do not by any means fill up this space. ("Das Kopfskelet der Urodelen." Morph. Jahrbuch, vol. iii. p. 149). By the expression "arrested growth" not much is said, if at the same time the cause of the arrest is left unstated. But what can be the cause why the whole organization remains stationary at the perennibranchiate stage, the sexual organs only undergoing further development? Surely only that law or force of heredity known by its effects, but obscure with respect to its causes, through which old phyletic stages sometimes suddenly reappear, or in other words, that power through which reversion takes place. It must not be forgotten that all these cases of "larval reproduction" in

the Tritons as an "adaptation" to a purely aqueous existence.<sup>4</sup> We could here only speak of "adaptation" if we took the word in a quite different sense to that in which it was first introduced into science by Darwin and Wallace. These naturalists thereby designate a gradual bodily transformation appearing in the course of generations in correspondence with the new requirements of altered conditions of life or, in other words, the action of natural selection, and not the result of a suddenly and direct acting transforming cause exerted but once on a generation.

Just because the word "adaptation" can be used in ordinary language in many senses, it is desirable that it should have only *one* precise signification, and above all that we should not speak of adaptation where scarcely any morphological

Amphibians appear suddenly. The present sexually mature form of the Axolotl has not arisen by the sexual maturity gradually receding in the ontogeny from generation to generation, but by the occurrence of single individuals which were sexually mature in the perennibranchiate stage, these having the advantage over the *Amblystomæ* in the struggle for existence under changed climatic conditions.

By admitting a reversion, we perfectly well explain why arrest at the perennibranchiate stage can be associated with complete development of the sexual organs; the assumption of an "arrested growth" leaves this combination of characters completely unexplained. Moreover, I am of opinion that the expressions "arrested growth" or "reversion" are of but little importance so long as the matter itself is clear.]

<sup>4</sup> See Haeckel's "Anthropogenic," p. 449.

change occurs, but only a kind of functional change in the sense used by Dohrn.<sup>25</sup> This is the case for example, when Forel<sup>26</sup> shows that fresh water Pulmonifera, the organization of which is attributed to the direct respiration of air, can nevertheless become settled in the greatest depths of mountain lakes through their lungs being again employed as gills. That not the least change in the lungs hereby takes place is shown by the observations of Von Siebold,<sup>27</sup> who saw the shallow water Pulmonifera using their lungs alternately for direct aërial and aquatic respiration, according to the amount of air contained in the water. If with Von Siebold we merely apply the word "adaptation" to such cases, this expression would lose the special sense which it originally conveyed, and the word would have to be abandoned as a *terminus technicus*; still, such cases may perhaps be spoken of as *physiological* adaptation.

In any case the reproductive "larvæ" of the Tritons as little present a case of true adaptation as the Axolotl, which occasionally becomes transformed into an Amblystoma. In both cases the transformation referred to is by no means indispensable to the life of the individual. Mature Tritons

<sup>25</sup> "Der Ursprung der Wirbelthiere und das Princip des Funktionswechsels," Leipzig, 1875.

<sup>26</sup> Bull. Soc. Neuchâtel. vol. viii. p. 192. . Reference given in "Troschel's Jahresbericht" for 1869.

<sup>27</sup> Sitzungsberichte d. math. phys. Klasse der Akad. d. Wiss. zu München, 1875. Heft i.



(devoid of gills) can exist, as I have myself seen, for many months, and probably also for a year in deep water, although adapted for purely pulmonary respiration; whilst Axolotls, as I have already mentioned, can live well for a year in shallow water poor in air. If their gills by this means become shrivelled up or completely disappear, even this is not adaptation in the Darwinian sense, but the effect of directly acting external influences, and chiefly of diminished use.

A case entirely analagous to that of Filippi's was observed by Jullien in 1869. Four female larvæ of *Lissotriton Punctatus* (Bell)—(synonymous with *Triton Tæniatus*, Schnl.), taken from a pool, proved to be sexually mature. They contained mature eggs in their ovaria ready for laying, and two of them actually deposited eggs. Four male larvæ found in the same pool, appeared to be equally developed with respect to size, but their testicles contained no free spermatozoa, but only sperm-cells.<sup>28</sup>

I have met with a third case of a similar kind mentioned by Leydig in his memoir, rich in interesting details, "on the tailed Amphibians of the Wurtemberg fauna."<sup>29</sup> Schreibers, the former director of the Vienna Museum, also found "larvæ" of Tritons with well-developed gills, but of the size of the "adult male individuals," and,

<sup>28</sup> Compt. Rend. vol. lxviii. pp. 938 and 939.

<sup>29</sup> Archiv f. Naturgeschichte, 1867.

as shown by anatomical investigation, with well "developed sexual organs," the ovaria especially being distended with eggs.

It is thus established that species which long ago reached the salamander stage in phyletic development, may occasionally degenerate to the perennibranchiate stage. This fact obviously makes my conception of the Axolotl as a reversion form appear much less paradoxical—indeed, the cases of reversion in Triton are precisely analagous to the process which I suppose to have taken place in the Axolotl. We have only to substitute *Amblystomas* for Tritons, to imagine the pool in which De Filippi found his "sexually mature Triton larvæ" enlarged to the size of the Lake of Mexico, and to conceive the unknown, and perhaps here transitory, causes of the reversion to be permanent, and we have all that is necessary, so far as we at present know, for the restoration of the Axolotl; we obtain a perennibranchiate population of the lake.

It has not yet been determined whether the perennibranchiate form of the Triton actually prevailed permanently in De Filippi's pool, since, so far as I know, this has not since been examined.

Let us, however, assume for an instant that this is really the case, and that there exists at that spot a colony of sexually reproductive perennibranchiate Tritons: should we wonder if a true Triton occasionally appeared among their progeny,

or if we were able to induce the majority of the individuals of this brood to become metamorphosed into Tritons by keeping them in shallow water? According to my view this is precisely the case of the Mexican Axolotl.

I need not, however, restrict myself to this in order to support my hypothesis, but must also directly combat the view hitherto received, since the latter is in contradiction with facts.

Did there really exist in the Axolotl a tendency to sudden phyletic advancement, then one fact would remain quite incomprehensible, viz. the sterility of the Amblystomas.

Out of about thirty Amblystomas obtained by Duméril down to the year 1870, there was not one in a state of sexual maturity; neither copulation nor deposition of eggs took place, and the anatomical investigation of single specimens showed that the eggs were immature, and that the spermatozoa, although present, were without the undulating membrane characteristic of the salamanders, but were not devoid of all power of movement, only, as established by Quatrefages, were "incompletely motile."<sup>30</sup>

So also the five Amblystomas about which I have been writing, show up to the present time no appearance of reproduction.

The objection raised by Sacc,<sup>31</sup> that the sterility

<sup>30</sup> Compt. Rend. vol. v. 1870, p. 70.

<sup>31</sup> Bull. Soc. Neuchâtel. vol. viii. p. 192. Referenc given in "Troschel's Jahresbericht" for 1869.

of the Amblystomas bred from Axolotls is attributable to "bad nourishment," is obviously of but little avail. How is it that the Axolotls, which are fed in a precisely similar manner, propagate so readily? Moreover, I am able to expressly assert that my Amblystomas were very well fed. It is true that they have as yet scarcely reached the age of two years, but the Axolotl propagates freely in the second year, and some of Duméril's Amblystomas were five years old in 1870.

This fact of the sterility is strongly opposed to the idea that these Amblystomas are the regular precursors of the phyletically advancing genus *Siredon*.<sup>31</sup> I will by no means assert that my

<sup>31</sup> [Eng. ed. It was mentioned in the German edition of this work that in the spring of 1876 a female Amblystoma of the Jardin des Plantes in Paris had laid eggs (see Blanchard in the Compt. Rend. 1876, No. 13, p. 716). Whether these eggs were fertile, or whether they developed was not then made known. Thus much was however at the time clear, that even if this had been the case, the reproduction of this Amblystoma would have been only an *exceptional* occurrence. At that time there were in the Jardin des Plantes Amblystomas which had been kept for more than ten years, and only on one occasion was there a deposition of eggs, and this by only one specimen. That I was correct in speaking of the "sterility" of these Amblystomas in spite of this one exception, is proved by the latest communication from the Jardin des Plantes. We learn from this (Compt. Rend. No. 14, July, 1879, p. 108) that in the years 1877 and 1878 none of the Amblystomas laid any more eggs, although all means were exerted to bring about propagation. In April, 1879, eggs were again laid by one female, and by a second in May. These eggs certainly developed, as did those of 1876, and produced tadpoles. These



theory of reversion actually explains the sterility, but it is at least not directly opposed to it. Mere reversion forms may die off without propagating themselves; but a *new form* called forth by the action of a phyletic vital force should not be sterile, because this is the precise "aim" which the vital force had in view. The conception of a vital force comprises that of teleology.

The sterility of *Amblystoma* moreover, although not completely explicable from our standpoint, can be shown to be a phenomenon not entirely isolated. In the above mentioned case of *Lissotriton Punctatus*, the female "larvæ" were certainly sexually mature and laid eggs, but the males of the same period contained in their testicles no fully developed spermatozoa.

Other cases of this kind are unknown to me; at the time when I made the experiments with butterflies already recorded (see the first essay), this point of view was remote, and I therefore neglected to examine the artificially bred reversion forms with respect to their organs of reproduction. But general considerations lead to the supposition that atavistic forms may easily remain sterile.

*Amblystomas* are therefore not absolutely, but indeed relatively sterile. Whilst the *Axolotl* propagates regularly and freely every year, this occurs with the *Amblystoma* but rarely and sparsely. The degree of their sterility can only be approximately established when we know the number of *Amblystomas* that have since been kept in the *Jardin des Plantes*. Unfortunately nothing has been said with respect to this.]

Darwin<sup>33</sup> finds the proximate causes of sterility in the first place in the action of widely diverging conditions of life, and in the next place in the crossing of individuals widely different in constitution. Now it is certainly deviating conditions of life which lead to the metamorphosis of the Axolotl, and from this point of view it cannot be surprising if we find those individuals sterile which show themselves so especially affected by these changed conditions as to revert to the salamander form.

By this it is not in any way meant to be asserted that reversion is invariably accompanied by sterility, and one cannot raise as an objection to my interpretation of the metamorphosis of the Axolotl, that a reproductive colony of Axolotls could never have arisen by reversion. On the contrary, Jullien's egg-depositing female Triton-larvæ show that also with reversion the power of reproduction may be completely preserved.<sup>34</sup> From the above-mentioned

<sup>33</sup> Origin of Species, 6th ed. p. 252.

<sup>34</sup> In plants also reversion forms show sterility in different degrees. Mr. Darwin has called my attention to the fact that the peloric (symmetrical) flowers which occasionally appear as atavistic forms in *Corydalis solida* are partly sterile and partly fertile. That in other causes of sterility, and above all by bastardizing, the reproductive power is lost in the most varying degrees, has been known since the celebrated observations of Kölreuter and Gärtner. [Eng. ed. An Orchid (*Catasetum tridentatum*) has the sexes separate, and the male flowers (*Myanthus barbatus*) differ considerably from the female (*Monachanthus viridis*); besides these, there occurs a form with bisexual flowers which must be considered as a reversion

general causes of sterility, it may even be inferred that fertility can be lost in different degrees, and it can be further understood to a certain extent why this fertility is more completely lost by reversion to the *Amblystoma*, than by the reversion of the Triton to the perennibranchiate form.

If in these cases the reversion is brought about by a change in the conditions of life, we may perhaps suppose that the magnitude of this change would determine the degree of fertility, and the preservation of the reversion form. Still more, however, would the fertility be influenced by the extent of the morphological difference resulting from the reversion. We know that the blending of very different constitutions (*e. g.* the crossing of different species) produces sterility. Something similar results from the sudden reversion to a stage of development widely different in its whole structure. Here also we have in a certain sense the union of two very different constitutions in one individual—a kind of crossing.

From this point of view it can in some measure be comprehended why sterility may be a result of reversion; on the other hand, we thereby obtain no explanation why, with the same amount of morphological difference, in one case complete sterility, and in another relative fertility occurs. The morphological difference between *Axolotl* and *Amblystoma*

(*Cat. tridentatum*) and *this is always sterile*. Darwin, "Fertilization of Orchids," 2nd ed. p. 199.]

is exactly the same as between Triton and its "sexually mature larva;" the difference between the two cases of reversion depends entirely upon the direction of the leap, that taken in the former case being precisely opposite in direction to that taken in the latter.

Herein might be sought the explanation of the different strength with which the reproductive power is affected; not indeed in the direction of the leap itself, but in the differences in the ontogeny which are determined by the differences in the direction of the leap. The reversion of the Triton to an older phyletic stage coincides with the arrest at a younger ontogenetic stage; or, in other words, the older stage of the phylogeny to which reversion takes place is still entirely comprised in the ontogeny of each individual. Each Triton is perennibranchiate throughout a long period of its life; the reverting individual simply reverts to the older phyletic stage by remaining at the larval stage of its individual development.

But it is quite different with the reversion of the Axolotl to the formerly acquired, but long since abandoned *Amblystoma* form. This is not retained in the ontogeny of Axolotl, but has been completely lost; for a long series of generations—so must we suppose—the ontogeny has always only attained to the perennibranchiate form. Now if at the present time certain individuals were compelled



to revert to the *Amblystoma* form, certainly no greater leap would have been made from a morphological point of view, than in the reversion of Triton to the perennibranchiate form, but at the same time the leap would be in another direction, viz. over a long series of generations back to a form which the species had not produced for a long period, and which had to a certain extent become foreign to it. We should thus have here also the grafting of a widely different constitution upon that of the Axolotl, or, if one prefers it, the commingling of two widely different constitutions.

Of course I am far from wishing to pretend that this "explanation" is exact; it is nothing more than an attempt to point out the direction in which the causes affecting the reproductive powers in different degrees are to be looked for. A deeper penetration into and special demonstration of the manner in which these causes bring about such results, must be reserved for a future period. For the present it must suffice to have indicated that there is an essential distinction between the two kinds of reversion, and to have made it to some extent comprehensible that this distinction may be the determining impulse with respect to the question of sterility. Perhaps the law here concealed from us may one day be thus formulated:—Atavistic individuals lose the power of reproduction the more completely, the greater the number of generations of their ancestors whose ontogeny no longer com-

prises the phyletically older stage to which the reversion takes place.

The hypothesis which interprets the transformation of the Axolotl as a case of reversion, thus holds out the possibility of our being able to comprehend the sterility of the Amblystomas arising in this manner, whilst, on the other hand, for the adherents of a phyletic vital force, not only is this observed sterility as Duméril expresses it "un véritable énigme scientifique," but an absolute paradox. We should expect such a directive and inciting principle to call into existence new forms having vitality and not destined to perish, the more so when it is concerned with a combination of structural characters which, when originating in another manner (viz. from other species of *Siredon*), have long since shown themselves to have vitality and reproductive power. We are indeed acquainted with species of *Amblystoma* which propagate as such, and each of which arises from an Axolotl-like larva. Thus we cannot regard the sterile Amblystomas produced by the Paris Axolotls as abortive attempts of a vital force—an interpretation which is certainly in itself already sufficiently rash.

Now if it be asked what change in the conditions of life could have led to the reversion in the Lake of Mexico <sup>35</sup> of the Amblystoma to the *Siredon*

<sup>35</sup> As we do not know the origin of the "Paris Axolotl" I must restrict myself in the following remarks to *Siredon Mexicanus* (Shaw).

form, I must admit that I can only offer a conjectural reply, having but a conditional value so long as it is not supported by a precise knowledge of the conditions there obtaining, and of the habits both of the Axototl and of the Amblystoma.

It may be supposed generally that reversion is brought about by the same external conditions as those which formerly produced the perennibranchiate stage. This supposition is in the first place supported by the experiments here recorded, since it is evidently the inducement to aërial respiration which causes the young Axolotl to revert to the Amblystoma form, *i.e.* the inciting cause under whose domineering influence the Amblystoma form must have arisen.

Here again the case is quite similar to that of seasonally dimorphic butterflies. Reversion of the summer brood to the winter form is there most easily caused by the action of cold, *i.e.* by the same influence as that under whose sway the winter form was developed.

We know indeed that reversion may also arise by the crossing of races and species, and I have attempted to show that reversion in butterflies may also be brought about by other influences than cold; but still the most probable supposition obviously is, that reversion would be caused by the persistent action of the same influences as those which in a certain sense created the perennibranchiate form. That the latter was produced under

the influence of an aquatic life there can be no doubt, and thus, in accordance with my supposition, the hypothetical *Amblystoma Mexicanum*, the supposed ancestral form of the Axolotl of the Mexican Lake, might have been caused to revert to the perennibranchiate form by a reduction in the possibilities of its living upon land, and by its being compelled to frequent the water.

I will not here return to the consideration of every other opinion *ab initio*. It is very advisable to distinguish between the mere impulses which are able to produce sudden reversion, and between actual transforming causes which result directly or indirectly in the remodelling of a species. Thus, it is conceivable *à priori* that reversion may occur by the action of an inciting cause having nothing to do with the origin of the phyletically older form. Temperature can certainly have played no part, or only a very small part, in the formation of the perennibranchiate form; nevertheless cold may well have been one of the inciting causes which induced the *Amblystoma* at one time to revert to the *Siredon* form, and we cannot at present consider De Saussure to be incorrect when he maintains that the low temperature of the Mexican winter might prevent that transformation (of the Axolotl into the *Amblystoma*) which would occur "in the warm reptile-house" of the Jardin des Plantes. He supports this view by stating that "Tschudi has found the *Amblystoma*" (of course



another species) "in the hottest parts of the United States." "On the Mexican plateau, however, it snows every winter, and if the lake does not actually freeze, its temperature must fall very considerably in the shallowest parts."

But although this view is not opposed by any theoretical considerations, I still hold it to be incorrect. I doubt whether it is temperature that has brought about the reverse transformation of the *Amblystoma* into the *Axolotl*, or which, according to De Saussure's conception, at the present time prevents the transformation of the *Axolotl* in the Lake of Mexico. I doubt this because *Amblystomas* are now known from all parts of the United States as far north as New York, a proof that a winter cold considerably greater than that of the Mexican plateau is no hindrance to the metamorphosis of the *Axolotl*, and that the genus does not show itself to be in this respect more sensitive than our native genera of *Salamandridæ*.

The following observations of De Saussure, in which he calls attention to the nature of the Mexican Lake, appear to me to be more worthy of consideration:—"The bottom of this lake is shallow, and one passes imperceptibly from the lake into extensive marshy regions before reaching solid ground; perhaps this circumstance makes the *Axolotl* incapable of reaching dry land, and prevents the transformation."

In any case the Lake of Mexico offers very

peculiar conditions for Amphibian life. My esteemed friend Dr. v. Frantzius has called my attention to the fact that this lake—as well as many other Mexican lakes—is slightly saline. At the time of the conquest of Mexico by Ferdinand Cortez, this circumstance led to the final surrender of the city, as the Spaniards cut off the supply of water to the besieged, and the water of the lake is undrinkable. The ancient Mexicans had laid down water-conduits from the distant mountains, and the city is still supplied with water brought through conduits.

Now this saltiness cannot in itself be the cause of the degeneration to the perennibranchiate form, but it may well be so in combination with other peculiarities of the lake. The narrowest part of the lake is the eastern, and it is only in this part that the Axolotl lives. Now in winter, violent easterly gales rush down from the mountains and blow continuously, driving the water before them to such an extent that it becomes heaped up in the western portion of the lake, where it frequently causes floods, whilst 2000 feet of the shallow eastern shore are often laid completely dry.<sup>36</sup>

Now if we consider these two peculiarities, viz. salineness and periodical drying up of a part of the bottom of the lake through continuous gales, we certainly have for the Axolotl, conditions of life

<sup>36</sup> Mühlenpfordt, "Versuch einer getreuen Schilderung der Republik Mejico," Hanover, 1844, vol. ii. p. 252.

which are only to be found in few species. One might certainly attempt to apply these facts in a quite opposite sense, and to regard them as unfavourable to my theory, since the retreat of the water from a great portion of the bottom of the lake would—so one might think—rather facilitate transition to a life upon land, and indeed compel the adoption of such a mode of existence. But we should thus forget that the exposed bottom of the lake is a sterile surface without food or place of concealment, and, above all, without vegetation; and further, that owing to the considerable salineness of the water (specific gravity = 1.0215),<sup>37</sup> the whole of the exposed surface must be incrustated with salt, a circumstance which would render it quite impossible for the creatures to feed upon land. Sodid chloride and carbonate are dissolved in the water in such considerable quantities, that they are regularly deposited upon the shores of the lake as a crust, which is collected during the dry season of the year and sent into the market under the name of “tequisquite” (Mühlenpfordt).<sup>38</sup>

Thus the supposition is not wanting in support, that peculiar conditions make it more difficult for the creature to obtain its food upon land than in

<sup>37</sup> [The specific gravity of sea water (Atlantic), according to the determinations of Mr. Buchanan on board the “Challenger,” at 15.56° C. varies from 1.0278 to 1.0240. That of the water of the Dead Sea is 1.17205.—Watts’ “Dict. of Chemistry,” vol. v., table, p. 1017. R.M.]

<sup>38</sup> *Loc. cit.* p. 252.

the water, and this alone may have been sufficient to have induced it to acquire the habits of a purely aquatic existence, and thus to revert to the perenni-branchiate or Ichthyodeous form.

But enough of supposition. We must not complain that we are unable from afar to discover with precision the causes which compelled the Axolotl to abandon the *Amblystoma* stage, as long as we are not able to explain the much nearer cases of reversion in Filippi's and Jullien's Tritons; nevertheless, in these cases also, the causes affecting the whole colony of Tritons must be general, since—at least in the case noticed by Filippi—the greater majority of the individuals remained in the larval condition. Experiments with Triton larvæ could throw greater light upon this subject; it would have in the first place to be established whether reversion could be artificially induced, and if so, by what influences.

From the previously mentioned experiments with butterflies, as well as from the results obtained with Axolotls, we should expect that in Tritons, reversion to the Ichthyodeous form would take place if we allowed the inciting cause, viz. the bathing of the gills and of the whole body with water, to act persistently, and at the same time withheld that influence under whose action the salamander form became developed, viz. the bathing of the gills, the skin, and the surfaces of the lungs with air.

Old experiments of this kind are to be met with,



but they were never carried on for a sufficient time to entirely allay the suspicion, that the specimens concerned would perhaps have undergone the ordinary metamorphosis if their existence had been prolonged.

Thus, Schreibers<sup>39</sup> relates that "by confining tadpoles of the salamander found at large in their last stage of growth, under water by means of an arrangement (net?), and feeding them with finely chopped earthworms, he was able to keep them for several months—and indeed throughout the winter—in this condition, and in this way to forcibly defer their final change, and their transition from the tadpole stage to that of the perfected creature during this period." It is not stated whether the animals finally underwent transformation, so that it cannot be decided whether we have here a case of reversion or simply one of retarded development. That metamorphosis may occur after a long period of time, is shown by experiments upon the tadpole of *Pelobates* conducted by Professor Langer in Vienna.<sup>40</sup> The creatures were kept in deep water in such a manner that they were not able to land, and by this means three out of a large number

<sup>39</sup> "Über die spezifische Verschiedenheit des gefleckten und des schwarzen Erdsalamanders oder Molchs, und der höchst merkwürdigen, ganz eigenthümlichen Fortpflanzungsweise des Letzteren." *Isis*, Jahrg. 1833, p. 527.

<sup>40</sup> The experiments referred to have not been made known; I am indebted for them to a written communication kindly furnished by an esteemed colleague.

of individuals had their metamorphosis delayed till the second summer; notwithstanding this, transformation then occurred.

It cannot be objected to my reversion hypothesis, that it opposes on the one side what on the other it postulates, viz. a *per saltum* change of structure. Reversion is characterized by the sudden acquisition of an older, *i.e.* a formerly existing phyletic stage. That reversion occurs is a fact, whilst nobody has hitherto been able to prove, or even to make probable, that a stage of the future (*sit venia verbo*) has been attained at once (*per saltum*).

Now if it is possible to find influences in the present conditions of life of the Axolotl which make it difficult or quite impossible for it to live upon land, and which therefore appear as incentives to the reversion to the Ichthyodeous form, the other portion of my hypothesis—the assumption that the Axolotl had become an Amblystoma at a former period—can also be supported by facts.

We know from Humboldt<sup>41</sup> that the level of the Lake of Mexico at a comparatively recent period was considerably higher than at present. We know further that the Mexican plateau was covered with forest, which has now been destroyed wherever there are human, and especially Spanish settlements. Now if we suppose that at some post-glacial period the mountain forests extended

<sup>41</sup> See Mühlensfordt's work already quoted, vol. i.

to the borders of the lake, at that time deep, with precipitous sides and much less saline, not only should we thus have presented different conditions of life to those at present existing, but also such as would be most favourable for the development of a species of salamander.

On the whole, I believe that my attempt to explain the exceptional metamorphosis of the Axolotl of the Mexican lake cannot be objected to as being a too airy phantasy. In any case it is the only possible explanation which can be opposed to that which supposes that the occasional transformation of the Axolotl is not reversion, but an attempt at advancement. This last assumption must, in my judgment, be rejected on purely theoretical grounds by those who hold that a sudden transformation of a species, when connected with adaptation to new conditions of life, is inconceivable—by those who regard adaptation, not as the sudden work of a magic power, but as the end result of a long series of natural, although minute and imperceptible causes.

If my interpretation of the facts be correct, there arises certain consequences which I may here briefly mention in conclusion.

First, with regard to more obvious results. If *Siredon Mexicanus*, Shaw, only by occasional reversion assumes the *Amblystoma* form, and never, or only exceptionally, propagates as such, but only as *Siredon*, the more recent systematists are not

justified in striking out the genus *Siredon* and in placing *S. Mexicanus* as an undeveloped form in the genus *Amblystoma*. So long as there exists not one only, but several species of *Siredon* which as such regularly propagate themselves, the genus exists ; and although we would not deprive systematists of all hope of these species of *Siredon* being one day re-elevated to *Amblystomæ*, it nevertheless better accords with the actually existing state of affairs if we allow the genus *Siredon* to remain as before among the genera of *Salaman-drina*, and to include therein all those species which, like the Paris Axolotl, *S. Mexicanus*, Shaw, and probably also *S. Lichenoides*, Baird, only exceptionally, or through artificial influences, assume the *Amblystoma* form, but without propagating regularly in this condition. On the other hand, we should correctly comprise under the genus *Amblystoma* all those species which propagate in this state regularly, and in which the perennibranchiate stage occurs only as a larval condition.

To arrive at a decision in single cases would chiefly concern the American naturalists, whose ever increasing activity may lead us to hope soon for a closer investigation of the reproduction of the numerous species of *Amblystoma* of their native country. I should rejoice if the facts and arguments which I have here offered should give an impetus to such researches.

The second consequence to which I may refer,



is of a purely theoretical nature, and concerns a corollary to the "fundamental biogenetic law" first enunciated by Fritz Müller and Haeckel. This, as is well known, consists of the following law:—The ontogeny comprises the phylogeny, more or less compressed and more or less modified.

Now according to this law, each step in phyletic development when replaced by a later one, must remain preserved in the ontogeny, and must therefore appear at the present time as an ontogenetic stage in the development of each individual. But my interpretation of the transformation of the Axolotl appears to stand in contradiction to this, since the Axolotl, which at a former period was an *Amblystoma*, retains nothing of the latter in its ontogeny. The contradiction is, however, only apparent. As long as we are concerned with an actual advance in development, and therefore with the attainment of a new step never formerly reached, the older stages will be found in the ontogeny. But this is not the case when the new stage is not an actual novelty, but formerly represented the final stage of the individual development; or, in other words, when we are concerned with the reversion, not of single individuals, but of the species as such, to the preceding phyletic stage, *i.e.* with a phyletic degeneration of the species. In this case the former end-stage of the ontogeny would be simply eliminated, and we should then only be able to recognize its former

existence by its occasional appearance in a reversion form. Thus, under certain conditions the Triton sinks back to the perennibranchiate stage; not in such a manner that the individual first becomes a Triton and then undergoes perennibranchiate re-modification, but simply, as I have already shown above, by its remaining at the Ichthyodeous stage and no longer attaining to the Salamander form. So also, according to my hypothesis, the salamandrine *Amblystoma Mexicanum*, formerly inhabiting the shores of the Lake of Mexico, has degenerated to the perennibranchiate stage; and the only trace that remains to us of its former developmental status is the tendency, more or less retained in each individual, to again ascend to the salamander stage under favourable conditions.

The third and last consequence which my interpretation of the facts entails, is the change in the part played by reversion in organic nature. Whilst atavistic forms have hitherto been known only as isolated and exceptional cases, interesting indeed in the highest degree, but devoid of significance in the course of the development of organic nature, a real importance in this last respect must now be attached to them.

I may assume that reversion can in two ways be effectual for the preservation or re-establishment of a living form. In the first place, where, as in Axolotl, the new and organically higher

form becomes untenable through external influences, instead of simply perishing—since advancement in another direction does not appear to be possible—a reversion of the species to the older and more lowly organized stage occurs. In the second place, the older phyletic form may not be abandoned while a newer form is being developed therefrom, but the former may alternate with the latter, as we see in the case of seasonally dimorphic butterflies. It can hardly be objected if I regard the alternation of the summer and winter form in this case as a periodic reversion to the phyletically older (winter) form.

Although the reversion of an entire species, such as I suppose to have been the case with the Axolotl, may be of rare occurrence, this is certainly not the case with periodic or cyclical reversion; the latter plays a very important part in the development of the various forms of alternating or cyclical propagation.<sup>42</sup>

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#### POSTSCRIPT.

In the previous portion of this essay it was pointed out that the causes to which I attributed the reversion of the hypothetical *Amblystoma Mexicanum* to the existing Axolotl, did not appear to me to amount to a complete explanation

<sup>42</sup> In the province of botany such a case has already been made known by Fritz Müller (Botan. Zeitung, 1869, p. 226;

of the phenomenon. In the first place these seemed to me too local, since they could only be applied with any certainty to the Axolotl of the lake of the Mexican capital, whilst the Paris Axolotls obtained from other parts of Mexico still required an explanation. On the other hand, these causes did not appear to me sufficiently cogent. Should we even learn subsequently that the Paris Axolotl is also derived from a salt lake which is exposed to similar winds to the Lake of Mexico, we still have in this peculiarity of the lakes only a cause tending to make it difficult for the larva to undergo metamorphosis, and to reach a suitable new habitat on the land. The impossibility of doing this, or the complete absence of such habitat, does not however follow as a necessary consequence.

It would obviously be a much more solid support for my hypothesis if it were possible to point to some physical conditions of the land which

1870, p. 149). I may be here permitted to quote a passage from the letter in which Dr. Müller calls attention to this interesting discovery. "As a proof of the possibility that a reversion form can again become a persistent character in a species or in the allied form of a particular district, I may refer you to an *Epidendrum* of the island of Santa Catharina. In all Orchids (with the exception of *Cypripedium*), only one anther is developed; in very rare cases well-formed anthers appear as reversions among the aborted lateral anthers of the inner whorl. In the *Epidendrum* mentioned, these are however always present."



there precluded the possibility of the existence of *Amblystomas*.

For a long time I was indeed unable to discover such causes, and I therefore concluded the previous portion of this essay and went to press. Afterwards, when residing in one of the highest valleys of our Alps in the Upper Engadine, an idea accidentally occurred to me, which I do not now hesitate to regard as correct after having tested it by known facts.

It happens that in the Upper Engadine there live only such *Amphibia* as persistently, or at least frequently resort to the water. I found frogs up to nearly 7000 feet above the sea, and Tritons at 6000 feet (Pontresina and Upper Samaden). On the other hand, the land-living mountain salamander, *S. Atra*,<sup>43</sup> was absent, although suitable stations for this species were everywhere present, and it would have wanted for food as little as do its allies the water-newts. Neither would the great elevation above the sea offer any obstacle to its occurrence, since it occa-

<sup>43</sup> [This species is interesting as being ovoviviparous, the young passing through the branchiate stage within the body of the mother. Some experiments, which were partially successful, were made by Fräulein v. Chauvin with a view to solve the question whether the branchiate stage could be prolonged by taking the larvæ directly from the mother before birth and keeping them in water. See "Zeit. für wissen. Zoo." vol. xxix., p. 324. R.M.]

sionally ascends to a height of 3000 metres (Fatiot).<sup>44</sup>

Now it is well known that the atmosphere of the Upper Engadine,<sup>45</sup> like that of other elevated Alpine valleys enclosed by extensive glaciers, is often extraordinarily dry for a long period, a condition which appears to me to explain why the black land-salamander is there absent,<sup>46</sup> whilst its near water-living ally occurs in large numbers. The skin of the naked *Amphibia* generally requires moisture, or else it dries up, and the creature is deprived of a necessary breathing apparatus, and often dies as rapidly as though some important internal organ had been removed. Decapitated frogs hop about for a long time, but a frog which escapes from a conservatory and wanders about for one night in the dry air of a room, is found the following day with dry and dusty skin half dead in some nook, and perhaps perishes in the course of another day if left without moisture.

All that we know of the biology of the *Amphibia* is in accordance with this. Thus, all the land-salamanders of southern Italy avoid the hot and

<sup>44</sup> See Fatiot, "Les Reptiles et les Batraciens de la haute Engadine." Geneva, 1873.

<sup>45</sup> I can remember at Upper Engadine a peculiar kind of preserved beef, prepared by simply drying in the air; also the mummification of entire human bodies by drying in the open air, as is practised at Great St. Bernard.

<sup>46</sup> "Faune des Vertébrés de la Suisse," vol. iii. "Histoire Naturelle des Reptiles et des Batraciens." Geneva, 1873.

dry air of summer by burying in the ground, where they undergo a summer sleep. This is the case with the interesting *Salamandrina Perspicillata*,<sup>47</sup> and with the land-living Sardinian Triton, the remarkable *Euproctus Rusconii*, Gené,<sup>48</sup> (*Triton Platycephalus*, Schreiber). With respect to *Geotriton Fuscus* I learn from Dr. Wiedersheim, who has studied the life conditions of this, the lowest European Urodelan, in its own habitat, that in Sardinia it sleeps uninterruptedly from June till the winter; whilst on the coast of Spezia and at Carrara, where it also occurs, it avoids the summer sleep in a very peculiar manner. It makes use of the numerous holes in the calcareous formation of that region, and for some months in the year becomes a cave-dweller. As soon as the great heat occurs, often in May, it withdraws into the holes, and again emerges in November during the wet weather. In these lurking holes it does not fall into a sleep, but is found quite active, and its stomach, filled chiefly with scorpions, shows that it goes successfully in search of food; the moist air of the holes makes it unnecessary for it to bury in the earth.

In the same sense it appears to me must be conceived the fact that the solitary species of frog

<sup>47</sup> See Wiedersheim, "Versuch einer gleichenden Anatomie der Salamandrinen." Würzburg, 1875.

<sup>48</sup> See Gené, "Memorie della Reale Acad. di Torino," vol. i.

of the Upper Engadine, *Rana Temporaria*,<sup>49</sup> the brown grass frog, is there much more a frequenter of the water than in the plains. It is true that I can find no remark to this effect in the excellent work of Fatiot, already referred to above, and I am therefore obliged to resort to my own observations, which, although often repeated, have always been carried on for only a short time. I was much struck with the circumstance that the Engadine frogs were to be found in numbers in the water long after the pairing season, which, according to Fatiot, lasts at most to the end of June. In the numerous pools around Samaden I found them in July and August, whilst in the plains they only take to the water at the time of reproduction, and seek winter quarters in the mud on the first arrival of this season. (Fatiot, p. 321.) In the Engadine they have therefore in some measure adopted the mode of life of the aquatic frogs, but this of course does not prevent them from returning in damp weather to their old habits and roving through meadows and woods.

After these considerations had made it appear to me very probable that the dry air of the Upper Engadine accounted for the absence of the black land-salamander, the question at once arose whether the absence of *Amblystomas* from the

<sup>49</sup> *Rana esculenta* never reaches Alpine regions, this species not having been found higher than 1100 meters. (Fatiot, *loc. cit.*, p. 318).



Mexican plateau might not perhaps be due to the same cause, *i.e.* whether such a dryness of the atmosphere might not perhaps prevail also in that region, so that Amphibia, or at least salamander-like Amphibia, could not long exist on the land. The height above the sea is still greater (7000 to 8000 feet), and the tropical sun would more rapidly dessicate everything in a country poor in water.

As I was at the time without any books that might have enlightened me on the meteorological conditions of Mexico, I wrote to Dr. v. Frantzius, who, by many years residence in Central America was familiar with the climate of this region, and solicited his opinion. I received the reply that on the high plains of Mexico an extraordinary dryness of the atmosphere certainly prevails. "The main cause of the dryness of the high plains is to be found in the geographical position, the configuration of the land, and the physical structure. The north-eastern trade-wind drives the clouds against the mountains, on the summits of which they deposit their moisture, so that no vapour is carried over; as long as the north-east trade-wind blows, the streams feeding the rivers flowing into the Atlantic Ocean are abundantly fed with water, whilst on the western slopes, and especially on the high plains, the clouds give no precipitation. In the second half of the year also, during our summer,

the so-called rainy season brings but little rain<sup>50</sup>—little in comparison with the more southern regions, where the heavy tropical thunderstorms daily deluge the earth with water. Mexico lies much too northerly, and does not reach the zone of calms, within which region these tropical rains are met with."

Thus, in the high degree of dryness of the air lasting throughout the year, I do not doubt that we have the chief cause why no *Amblystomas* occur on these elevated plains; they simply cannot exist, and would become dried up if taken there, supposing them not to be able to change their mode of life and to take to the water. If therefore in former times *Amblystomas* inhabited Mexico, the coming on of the existing climatic conditions left them only the alternative of becoming extinct, or of again taking to the aquatic life of their *Ichthyodeous* ancestors. That this was not *directly* possible—that the *Amblystoma* form was not able to become aquatic without a change of structure, is shown by the fact that even in the Lake of Mexico no *Amblystoma* occurs. A retreat to an aqueous existence could, as it appears, only be effected by complete reversion to the *Ichthyodeous* form, which then also took place.

But my hypothesis of the transformation of the

<sup>50</sup> See also the excellent work upon Mexico by Mühlenpfordt already quoted, vol. i., pp. 69—76.

Axolotl not only requires the proof that Amblystomas cannot exist under present conditions in Mexico, but also the further demonstration that at a former period other conditions prevailed there, and these of such a nature as to make the existence of land-salamanders possible.

With respect to my question, whether we might not perhaps assume that at some post-glacial period the conditions of atmospheric moisture on the high plains of Mexico were essentially different from those at present prevailing, I recollected Dr. v. Frantzius and the above-quoted observation of Humboldt's,<sup>51</sup> who discovered in the neighbourhood of the Lake of Tezenco (Mexico) distinct evidence of a much higher former level of the water. "All such elevated plains were certainly at a former period so many extensive water-basins, which gradually became filled, and are still filling up with detritus. The evaporation from such large surfaces of water must at that time have caused a very moist atmosphere, favourable to vegetation and adapted for the life of naked Amphibia."

From this side also my hypothesis thus receives support, and we may assume with some certainty that at the beginning of the diluvial period<sup>52</sup> the

<sup>51</sup> "Essai politique sur le Royaume de la Nouvelle Espagne," 1805, p. 291.

<sup>52</sup> [The expression made use of by the author, viz. "Diluvialzeit," would perhaps be more in harmony with the views of English geologists if rendered as the "pluvial period,"

woods surrounding the Mexican lakes were inhabited by Amblystomas, which, as the lakes subsequently became more and more dried up and the air continually lost moisture, found it more difficult to exist on the land. They would at length have completely died out, had they not again become aquatic by reversion to the Ichthyodeous form. It may perhaps be supposed that the above-mentioned physical conditions—desolate, salt-incrusted shores—co-operated in the production of the reversion, by making it difficult for the larvæ to quit the water; but we can only judge with certainty upon this point when, by means of experiment, we have discovered the causes which produce reversion in the Amphibia.

#### ADDENDUM.

I have lately met with another interesting notice on the reproduction of the native North American Amblystomas. Professor Spence F. Baird, of Washington, has often observed the

thereby indicating the period of excessive rainfall which, according to Mr. Alfred Tylor, succeeded to and was a consequence of the thawing of the great glaciers which accumulated during the last glacial epoch. There is abundant evidence to show that during the latter period glacial action extended in North America at least as far south as Nicaragua. See Belt on "The Glacial Period in North America," Trans. Nova Scotian Inst. of Nat. Sci. 1866, p. 93, and "The Naturalist in Nicaragua," pp. 259—265. R.M.]



development from the egg of various species, and especially of *Amblystoma Punctatum* and *A. Fasciatum*. His observations do not appear to be as yet published, so that I was unable to discover any account of the development of *Amblystoma* in existing literature.<sup>53</sup> I am authorized to extract the following brief data from a letter addressed to Dr. v. Frantzius.

In order to deposit their eggs the Amblystomas go into the water, where the eggs are laid enclosed in a jelly-like mass, but never more than fifteen to twenty together. The spherical eggs are very large, perhaps a quarter of an inch in diameter. They soon develop into a *Siredon*-like larva, which remains several months in this condition. The gills then shrivel up, the creature begins to crawl, and gradually passes through the different transformations to the complete Amblystoma form.

It appears from this communication that the Amblystomas lay much larger and much fewer eggs than the Axolotl, and that their development throughout resembles that of our salamanders.

In concluding I may mention an anatomical fact which most strongly supports my view that the Mexican Axolotl is a reverted Amblystoma. I learn from Dr. Wiedersheim that the Axolotl possesses the "intermaxillary gland" which occurs

<sup>53</sup> [Eng. ed. A memoir by Samuel Clarke has since been published upon the embryonic development of *Amblystoma punctatum*, Baird. Baltimore, 1879.]

in all the land Amphibia. This organ, lying in the intermaxillary cavity, appears, whenever it occurs, to produce a kind of birdlime, *i. e.* a very glutinous secretion, which serves to attach the prey to the rapidly protrusible tongue. Although this secretion may perhaps also have another function, from the absence of the intermaxillary gland in all exclusively aquatic Amphibia, it follows that it must be devoid of importance for, and inapplicable to feeding in the water. The intermaxillary gland is absent in all *Perennibranchiata* and *Derotremata* which Wiedersheim has hitherto investigated, viz. in *Menobranchus*, *Proteus*, *Siren*, *Cryptobranchus*, *Amphiuma*, and *Menopoma*, all of which are indeed without the cavity in which the gland is situated in the *Salamandrina*, *i. e.* the *cavum intermaxillare*.

Now in the *Salamandrina* the gland appears at an early stage. It is possessed in a well-developed state by the larvæ both of species of *Triton* and of *Amblystoma*, where indeed the glandular structure completely fills the *cavum intermaxillare*.

Were the Axolotl a species retarded in phyletic development, the presence of a gland which does not occur in any other *Perennibranchiata*, and which is only of use for life upon land, would be quite inexplicable.

The matter becomes still more enigmatical through the fact that the gland, although present,

is quite rudimentary. Whilst in the *Salamanca-drina* the capacious intermaxillary cavity is entirely filled by the tubes of the gland in question, in Axolotl this cavity is almost completely filled with a closely woven connective tissue, in which there can only be found a small number of gland-tubes—in the extreme front, and at the base immediately over the intermaxillary teeth—these tubes agreeing in the details of their histological structure with the elements of the same gland in the *Salamandridæ*.

I give these anatomical details from Dr. Wiedersheim's verbal communication. An amplified account will subsequently appear in another place.<sup>54</sup>

An explanation of this rudimentary intermaxillary gland in the Axolotl only appears to me possible on the supposition that the latter is an atavistic form. From this point of view it is evident that the gland already present in all *Amblystoma*-larvæ must have been taken over by the perenni-branchiate form of the existing Axolotl, through the reversion of the hypothetical *Amblystoma Mexicanum* of the "diluvial period."<sup>55</sup> It can also be easily understood that this organ would become more and more rudimentary in the course of time, since it has no further use in the water,

<sup>54</sup> [Eng. ed. See this author's work, "Das Kopfskelet der Urodelen." Leipzig, 1877, p. 149.]

<sup>55</sup> [See preceding note 52. R.M.]

and the gap thus arising in the formerly present *cavum intermaxillare* would become filled with connective tissue.

While the German edition of this work was going through the press I obtained, through the kindness of my friend Dr. Emil Bessels of Washington, the Mexican memoir upon the new Axolotl,<sup>56</sup> which even in Mexico regularly, or at least in many cases, becomes developed into the Amblystoma form.

The facts are briefly as follows:—The small Lake of Santa Isabel is some hours' journey from the Mexican capital. In this lake there lives a species of Axolotl which had hitherto remained unknown, and was described by Señor Velasco as *Siredon Tigrinus*. This species propagates itself indeed in the Axolotl state, but in many cases it becomes transformed into Amblystoma and takes to the land. Although propagation in the Amblystoma condition was not observed, it can hardly be doubted that it also propagates in this form.

At first sight these facts appear to refute my hypothesis, that the extreme dryness of the air of the Mexican plateau precludes the existence of land Amphibia. Nevertheless I do not abandon this hypothesis for the former one, since a closer study of the data furnished by Velasco confirms rather than refutes my supposition.

Velasco expressly corroborates the statement

<sup>56</sup> See note 2, p. 566.



that the Axolotl hitherto known from the great Mexican lake which never dries up (Lake of Xochimilco and Chalco), is only met with in its native habitat in the *Siredon* form, *i.e.* as *Siredon Humboldtii*. According to Velasco the cause of the frequent assumption of the *Amblystoma* form by the new *Siredon Tigrinus*, is to be found in the local conditions of life of this species. The Lake Santa Isabel is shallow, its greatest depth amounting to three meters, and it is liable to a periodical drying up, which is so complete that one can pass dry-shod through it in several places. The species must therefore have long since died out had it not been able to adapt itself periodically to a land life. Now it could have become transformed into a land Amphibian—as Señor Velasco observed—at various stages of growth; and indeed this author believes that “the Creator has implanted an instinct in this creature,” which enables it to always undergo metamorphosis at the right time.

This last assumption may or may not be taken as correct, but this much is established, *viz.* that numerous individuals of this species take to the land, and remain there during a period of many months.

But does this contain the proof that salamander-like animals are actually able to lead a land life in Mexico—that the dry air is advantageous; or at least supportable to them? It does not appear so

to me, but rather that all which has been reported of this Amblystoma by Señor Velasco goes to show that the animal does not, properly speaking, live upon land like the North American Amblystomas, or like our land-salamanders, but that *it only experiences a summer sleep lasting over the period of drought*. These Amblystomas were observed as they left the dried-up lake at night in order to seek some moist lurking-place in the neighbourhood, where they might remain concealed. They are only known in the villages situated near the lake, and were only seen there at large just when they were wandering from the lake to their place of concealment. At other times they were mostly found in the earth, buried under walls, the pavement of the market-place, &c. When laying down a line of railway, a workman found in the earth a whole nest of twelve Amblystomas lying close together. All these are not mere lurking-holes which could be abandoned at any moment ; it would rather appear that we have here places of refuge for the entire duration of the period of drought, and that these would only be forsaken when the water of the rainy season penetrated the soil. I am not myself in a favourable position for investigating these suppositions more closely, but this could be done by Señor Velasco, who lives in Mexico, and science would be much indebted to him if he would examine as precisely as possible into the habits and conditions of life of

this, and of the other species of Mexican Axolotls. Unfortunately this gentleman can, it would appear, have seen only the French publications upon the transformation of the Axolotl, and could not therefore have asked himself questions arising from my conception of the facts; otherwise many of his observations would have led to more definite results. The above conclusion can however be still further supported by Señor Velasco's data.

One might indeed insist that with us also the land-salamanders conceal themselves in moist places during dry weather, and often lie hidden, as in Mexico, in a hole, in a cluster of as many as ten together; but with us they leave their lurking-place from time to time and go in search of food. Señor Velasco mentions nothing with respect to this. What especially struck me was the statement that the Mexican *Amblystomas* *were also to be found in the water.*<sup>67</sup> When Lake Santa Isabel

<sup>67</sup> [Prof. Semper also remarks ("Animal Life," note 47, p. 430) with reference to the Axolotl of Lake Como in the Rocky Mountains, which he states always becomes transformed into *Amblystoma Mavortium*, that this metamorphosis "takes place in the water, and the Amblystomas, so long as they are little, actually live exclusively in the water, as I know by my own experience. A young Amblystoma which I kept alive for a long time, never went out of the water of its own free will, while one nearly twice as large lives entirely on land and only takes a bath now and then. It always goes into the water when the temperature of the air in the cellar, in which my aquaria stand, falls below that of the water—down to about 6° or 8° C." This statement appears to suggest that the effect of tempera-

is drained, the fishermen stretch large nets across the exit channels, and in these they not only find ordinary Axolotls, but also some "*sin aretes*," which they also designate "*mochos*," *i. e.* hornless Axolotls, because they have no gills, but have already reached the Amblystoma stage. Our land-salamanders live in the water only as larvæ, but they also love and require moisture. Only the female enters the water when she wants to deposit her young (eggs with mature larvæ), and then only at the margin of shallow pools or small brooks. The Mexican Amblystoma thus much more resembles in its habits our water-salamanders

ture may be a factor in some way concerned in these interesting cases of transformation, and would in any case be well worthy of experimental investigation. Some further details concerning the *Siredon Lichenoides* of Lake Como have been recently published by Mr. W. E. Carlin (Proc. U.S. National Museum, June, 1881). The lake, which is shallow, is fed by a constant stream of fresh water, but the water of the lake is intensely saline. The *Siredon* never enter the fresh water stream, but congregate in large numbers in the alkaline waters of the lake. "When about one hundred and fifty were placed in fresh water they seemed to suffer no inconvenience, but it had a remarkable effect in hastening their metamorphosis into the Amblystoma form. Of an equal number kept in fresh water and in the lake water, quite a change occurred with the former after twenty-four hours, while the latter showed no change after several days of captivity. Those that were kept well fed in jars usually began to show a slight change in from two to three weeks, and all of them completed the change into the Amblystoma inside of six weeks, while in some kept, but not specially fed, there were but three changes in three months." (Nature, Aug. 25th, 1881, p. 388). R.M.]



(Tritons), which remain in the water at least during the whole period of reproduction. These also leave the water later, and, like the land-salamander, seek concealment in the earth. They have this habit also in those districts which possess a very dry atmosphere; and especially in the Engadine, where I first conceived the idea of taking into account the dryness of the air, I found in the pools at the end of August and the beginning of September only larvæ of Tritons. The older Amphibians must therefore have been on the land, presumably in their places of winter concealment.

From what we have hitherto learnt from Señor Velasco, the mode of life of *Amblystoma Tigrinum* must resemble that of our Tritons, although its structure is that of a land-salamander. I would thus offer the following explanation of the facts at present known:—Owing to the periodic drying up of the lake of Santa Isabel, the *Siredon Tigrinus* would be again compelled to undergo metamorphosis. Whether this was formerly entirely abandoned, or whether it always occurred in solitary individuals, is almost immaterial; in any case the habit of metamorphosis must have been very rapidly acquired through natural selection, and must have again become general, if the faculty was only present in the species, although latent. Through the dryness of the air, the *Amblystomas* that had taken to the land would be compelled to bury themselves at once, and to remain asleep till

the recurrence of the rainy season, when they would hasten back into the water and would there live as a species of Triton.

Now one might feel inclined to ask why the species of the great Mexican lake has not also taken to this mode of life. To this it may be simply replied that the water of this lake never dries up, and that the Axolotls have thus never been reduced to the alternative of undergoing metamorphosis or of perishing. If therefore the conditions of existence in water were more favourable than on land, the tendency to abandon metamorphosis would increase from generation to generation, and the deportment at present observed would finally result, *i.e.* propagation would take place exclusively in the Axolotl state. As has already been mentioned above, the latest observations of Velasco furnish further confirmation that the Axolotl of the great lake is never met with in the Amblystoma condition, "although it (the Axolotl) is brought daily from Mexico into the market throughout the whole year." I should not however regard it as a refutation of my view if prolonged investigation should show that this species also (*Siredon Humboldtii*) occasionally developed into an Amblystoma; on the contrary, it would not at all surprise me if such cases of reversion occurred in Mexico as well as in Europe. The fact that an immense majority of the Amphibians propagate in the Axolotl state

would not be thereby affected, and would still require an explanation : this I am still inclined to see in the dryness of the air of the high plains, which is so unfavourably adapted for a life passed entirely on land.

## IV.

### ON THE MECHANICAL CONCEPTION OF NATURE.

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#### INTRODUCTION.

IN the first of the three preceding essays it was attempted to solve the question whether the transformations of a given complex of characters in a certain systematic group could be completely explained by the sole aid of Darwinian principles. It was attempted to trace the origin of the marking and colouring of the Sphinx-caterpillars to individual variability, to the influences of the environment, and to the laws of correlation acting within the organism. These principles as applied to the origin of a certain well-defined, although narrowly restricted range of forms, were tested in order to see whether they were alone sufficient to explain the transformation of the forms.

It appeared that this was certainly the case. In all instances, or at least where the facts necessary to obtain a complete insight were available, the transformations could be traced to these known factors; there remained no inexplicable residual phenomena, and we therefore had no



reason for inferring the existence of some still unknown modifying cause lying concealed in the organism. In this region of the marking and colouring of caterpillars, the assumption of a phyletic vital force had to be abandoned, as being superfluous for the explanation of the facts.

In the second essay the attempt was next made with reference to double form-relationship, as presented for observation in metamorphic insects, to draw conclusions as to the causes of the transformations. It appeared here that form- and blood-relationship do not always coincide, since the larvæ of a species, genus, or family, &c., may show quite different form-relationships to their imagines. These facts alone told very decisively against the existence of an internal developmental power, so that the latter had likewise to be set aside by the method of elimination, since the observed incongruences as well as the congruences of form-relationship, found sufficient explanation in the action of the environment on the organism.

This investigation thus also led to the denial of a phyletic vital force.

In the third essay I finally sought to prove that the only case of transformation of one species into another at present actually observed<sup>1</sup>, could

<sup>1</sup> [Some experiments on the transformation of the Crustacean *Artemia Salina* into *A. Milhausenii* by gradually increasing the saltiness of the water, and conversely, the transformation of

not without further evidence be interpreted as the result of the action of a phyletic vital force, but that more probably we had here only an apparent case of new formation, which was in reality but a reversion to a stage formerly in existence.

If this last investigation removes the only certain observation which could have been adduced in favour of the hypothesis of a phyletic vital force, so also do the two former essays show that this hypothesis, at least in the case of insects, must be abandoned as inadequate.

The question now arises whether this conclusion, based on such a limited range of inquiry, can also be applied to the other groups of the organic world without further evidence.

The supporters of a principle of organic development will deny this in each individual case, and will demand special proof for each group of organisms; I believe this position, however, to be incorrect. Here, if anywhere, it appears to me justifiable to apply the conclusions inductively from special cases to general ones, since I cannot at all see why a power of such pre-eminent and fundamental importance as a phyletic vital force should have its activity limited to solitary groups

*A. Milhausenii* into *A. Salina* by diminishing the saltiness of the water, have been made by Schmankewitsch (Zeitschrift f. wiss. Zool. xxv. Suppl. 103 and xxix. 429), but the changes which occur here are much less considerable than in the case of the Axolotl. [R. M.]

in the organic world. If such a power exists it must be the inciting cause of organic development in general, and must be equally necessary in every part of creation, as no advancement could take place without it. In this case, however, the force would be recognizable and demonstrable at every point; the phenomena should nowhere stand in opposition to its admission, and should in no case be explicable or comprehensible without it. The same laws and forces which caused the development of one group of forms must underlie the development of the whole organic world.

I therefore believe that we are correct in applying to the whole living world the results furnished by the investigation of insects, and in thus denying the existence of an innate metaphysical developmental force.

There is, however, a quite distinct method which leads to the same results, and to the preliminary, if not to the complete and definitive rejection of such a principle; *the admission of this power is directly opposed to the laws of natural science*, which forbid the assumption of *unknown* forces as long as it is not demonstrated that *known* forces are insufficient for the explanation of the phenomena. Now nobody will assert that this has in any case been proved; the test of applying the known factors of transformation has only just commenced, and wherever it has been made they have proved sufficient as causal forces.

Thus, even without the foregoing special investigations we should deny a phyletic vital force ; the more so as its admission is fraught with the greatest consequences, since it involves a renunciation of the possibility of comprehending the organic world. We should, on this assumption, at once cut ourselves off from all possible mechanical explanation of organic nature, *i. e.* from all explanation conformable to law. But this signifies no less than the renunciation of all further inquiry ; for what is investigation in natural science but the attempt to indicate the mechanism through which the phenomena of the world are brought about ? Where this mechanism ceases science is no longer possible, and transcendental philosophy alone has a voice.

This conception represents very precisely the well-known decision of Kant :—" Since we cannot in any case know *à priori* to what extent the mechanism of Nature serves as a means to every final purpose in the latter, or how far the mechanical explanation possible to us reaches," natural science must everywhere press the attempt at mechanical explanation as far as possible. This obligation of natural science will be conceded even by those who lay great stress upon the necessity for assuming a designing principle. Thus, Karl Ernst von Baer states that we have no right "to assert of the individual processes of Nature, even when these evidently lead to a definite result,



that some Mind has originated them designedly. The naturalist must always commence with details, and may then afterwards ask whether the totality of details leads him to a general and final basis of intentional design."<sup>2</sup>

But even if we are precluded on these grounds only from assuming the existence of a directive power, *i. e.* a phyletic vital force, for explaining detailed phenomena, and are at the same time debarred from the possibility of arriving at a physical or mechanical explanation—which amounts to no less than the abandoning of the scientific position—it certainly cannot be asserted that the development of the organic world is already conceived of as a mechanical process. We rather acquiesce in the belief that the processes both of organic and of inorganic nature depend most probably upon purely causal powers, and that the attempt to refer these to mechanical principles should not therefore be abandoned. There is no ground for renouncing the possibility of a mechanical explanation, and the naturalist *must not* therefore resign this possibility; for this reason he cannot be permitted to assume a phyletic power so long as it is not demonstrated that the phenomena can never be understood without such an assumption.

<sup>2</sup> "Reden und kleinere Aufsätze, Th. II.: Studien aus dem Gebiete der Naturwissenschaften." St. Petersburg, 1876. P. 81.

It cannot be raised as an objection that even for the explanation of individual life a vital power was long ago admitted, as there was not then sufficient material at hand to enable the phenomena of life to be traced to physical forces. It is now no longer questionable that this assumption was a useless error—a false method—at the time when made certainly very excusable, since the aspect of the question was then, owing to the imperfect basis of facts, very different to the present analogous question as to the causes of derivative development. Thus, although it is now easy to prove this assumption to be erroneous, it was in the former sense correct, as it was in accordance with the existing state of knowledge. At that time there was hardly one of the numerous bridges which now connect inorganic with organic nature, so that the supposition that life depended upon forces which had no existence outside living beings was sufficiently near.

In any case the philosophers of that period cannot be blamed for filling up the gaps in the existing knowledge by unknown powers, and in this manner seeking to establish a finished system. The task of philosophy is different to that of natural science; the former strives at every period to set up a completely finished representation of the universe in accordance with the existing state of knowledge. Natural science on the other hand is only concerned in collecting this knowledge;

she need not therefore always finish off, and indeed can never close her account, since she will never be in a position to solve all problems.<sup>3</sup> But science must not for this reason pronounce any question to be insoluble simply because it has not yet been completely solved; this she does, however, as soon as she renounces the possibility of a mechanical explanation by invoking the aid of a metaphysical principle.

That this is the correct mode of scientific investigation is seen by the abandoning of the (ontogenetic) vital force. The latter is no longer admitted by anybody, now that we have turned from mere speculation to the investigation of Nature's processes; nevertheless its non-existence has not been demonstrated, nor are we yet in a position to prove that all the phenomena of life must be traced to purely physico-chemical processes, to say nothing of our being actually able to thus trace them. Von Baer also states "that the abolishment of the vital force is an important advance; it is the reduction of the phenomena of life to physico-chemical processes, although these

<sup>3</sup> This obviously does not imply that the naturalist should not investigate Nature's processes, and not only correlate these, but also work them up into a universal conception; this is indeed both desirable and necessary if natural knowledge is to be regarded in its true value. The naturalist by this means becomes a philosopher, and the vitality of the so-called "natural philosopher" has been inspired, not by the necessity for investigation, but by philosophy proper.

indeed still contain many gaps." He points out how very far we are still removed from being able to reduce to physical causes, the processes through which the fertilized yolk of an egg becomes developed into a chicken.

How comes it therefore that we all have a conviction that such a complete reduction will in time become possible, or if not this, that the development of the individual depends entirely upon the same forces which are in operation without the organism? For what reason have we rejected the "vital force"?

Simply because we see no reason for assuming that known forces are insufficient for explaining the phenomena, and because we are not justified in admitting directive forces as long as we have any hope of one day furnishing a mechanical explanation.

But if it is not only permissible, but even necessary, to explain the *ontogenetic* vital power by known forces, and to commence to indicate the mechanism which produces the individual life, why should it not be equally necessary to abandon that assumption of a *phyletic* vital force which stifles any deeper inquiry, and to attempt to point out that here also the co-operation of mechanical forces has brought about the multitudinous and wonderful phenomena of the organic world?

The renunciation of the old vital force was certainly an immediate consequence of the acqui-



sition of new facts—of the knowledge that the same compounds which compose organic bodies can be produced without the latter. This discovery, due to Wöhler and his followers, showed that organic products could be prepared artificially.<sup>4</sup> In brief, the decline of the vital force followed from the knowledge that at least one portion of the processes of life was governed by known forces.

But in the domain of the development of the organic world have we not quite analogous proofs of the efficacy of known forces? Is not the *variability* of all types of forms a fact? and must not this under the action of natural selection and heredity lead to permanent changes? Has not the problem of explaining the subserviency of all organic form to law as a *result* without invoking its aid as a *principle* been thus successfully solved? It is true that we have not directly observed the process of natural selection from beginning to end; neither has anybody directly

<sup>4</sup> [The discovery here referred to is the synthesis of urea by Wöhler in 1828 (Pogg. Ann. xii., 253; xv. 619), by the molecular transformation of ammonium cyanate. Since that period large numbers of organic syntheses have been effected by chemists, and many of the compounds formerly supposed to be essential products of life have been built up in the laboratory from their inorganic elements. The division of chemistry into "organic" and "inorganic" is thus purely artificial, and is merely retained as a matter of convenience, the former division of the science being defined as the chemistry of the carbon compounds. R. M.]

observed the mode in which the heat of the animal body is generated by the processes of combustion going on in the blood and in the tissues; nevertheless, this is believed as a certainty, and a "vital force" is not invoked.

Now the above-mentioned Darwinian principles of transmutation are certainly not simple forces of nature like those underlying the development of the individual, *i. e.* chemico-physical forces, and it cannot be said *à priori* whether in one of these principles—perhaps in variability or in correlation—there may not lie concealed a metaphysical principle in addition to the physical forces. In fact it has lately been asserted by Edward von Hartmann<sup>5</sup> that the theory of selection is not a mechanical explanation, since it combines forces which are only partly mechanical and in part directive.

It must therefore be next investigated whether this assertion is tenable.

<sup>5</sup> "Wahreit und Irrthum im Darwinismus." Berlin, 1875.

I.

ARE THE PRINCIPLES OF THE SELECTION  
THEORY MECHANICAL?

EDWARD VON HARTMANN may justly claim that his views should be considered and tested by naturalists.<sup>1</sup> He would be correctly classed with

<sup>1</sup> [Eng. ed. I have been reproached by competent authorities for having clothed my ideas upon the theory of selection in the form of a reply to Von Hartmann. I willingly admit that this author cannot be considered as the leader of existing philosophical views upon the theory of descent in Germany; Frederick Albert Lange has certainly a much greater claim to this position. Lange does not however combat this theory; he accepts and develops it most beautifully and lucidly on a sound philosophical basis in such a manner as has never been done before from this point of view ("Geschichte des Materialismus," 3rd. ed., 1877, vol. ii. pp. 253—277). On most points I can but agree with Lange. Von Hartmann, however, whose objections appeared to me to be supported by a wide scientific knowledge, afforded me a suitable opportunity of developing my own ideas upon some essential points in the theory of selection. In this sense only have I attempted to interfere with this author, the refutation of his views, as such, having been with me a secondary consideration.] [The chief exponent of the doctrine of organic evolution in this country is Mr. Herbert Spencer, in whose "Principles of Biology," vol. i. chap. xii., will be found a masterly treatment of the theory of descent from a "mechanical" point of view. R. M.]

those philosophers who have approached this question with a many-sided scientific preparation. It can nevertheless be perceived in his case how difficult, and indeed how impossible, it is to estimate the true value of the facts furnished by the investigation of nature, when we attempt to take up only the results themselves, without being practised in the methods by which these are reached, *i. e.* without being completely at home in one of the scientific subjects concerned through one's own investigations. It appears to me that the denial of the purely mechanical value of the Darwinian factors of transformation arises in most part from an erroneous classification of the scientific facts with which we have to deal. There can certainly be no mistake that the entire philosophical conception of the universe, as laid down by Von Hartmann in his "Philosophy of the Unconscious," is unfavourable to an unprejudiced estimate of scientific facts and to their mechanical valuation.

Variability, heredity, and above all correlation, would not be regarded by Von Hartmann as purely mechanical principles, but he would therein assume a metaphysical directive principle.

In the first place, as regards variability, Von Hartmann endeavours to show that it is only a quite unlimited variability which suffices for the explanation of necessary and useful adaptations by means of selection and the struggle for ex-



istence. But this does not exist—variation rather takes place in a fixed direction only (in Askenasy's sense), and this can be nothing else than the expression of an innate law of development, *i.e.* a phyletic vital force.

This deduction appears to me in two ways erroneous. In the first place it is incorrect that a quite unlimited variability is a postulate of the theory of selection, and in the next place the admission of variability, which is in a certain sense "fixed in direction," does not necessitate the assumption of a phyletic vital force.

A mere unsettled variability, uniform in all possible directions, is, according to Von Hartmann, necessary for the theory of selection, because only then does the variability offer a certain guarantee "that under given conditions of life the variations necessary for complete adaptation will not be wanting." But it is hereby overlooked that the new life conditions to which the adaptation must take place are as little fixed and unchangeable as the organism itself. In such a case of transformation we have not to deal with a type of organization which was before fixed and immutable, and which has to be squeezed into new life-conditions as into a mould. The adaptation is not one-sided, but mutual; a species in some measure selects its new conditions of life, corresponding with those possible to its organization, *i.e.* with the variations actually occurring. I will choose

an instance which will even be conceded by Von Hartmann as being only explicable by natural selection, viz., a case of mimicry.

Supposing that among the South American *Heliconiidae* there occurred a species of *Pieris* which had no resemblance to these protected butterflies, either in form, marking, or colouring ; who can deny that it would be most useful to this species to acquire the form and colouring of a Heliconide, and thus, by taking to new conditions of life, to avoid the persecutions of its foes ? But if the physical nature of the Pieride concerned precluded the occurrence of Heliconoid variations, would this incapability of insinuating itself into these new conditions necessitate the decline of the species ? Could not its existence be secured in some other manner ? could not the destruction of numerous individuals by foes be compensated for by increased fertility ? to say nothing of the numerous other means through which the number of surviving individuals might become increased, and the existence of the species secured. This case is not arbitrarily chosen ; in the districts where the *Heliconiidae* occur there are actually a large number of Whites which do not possess the protective colours of the former nauseous family. In the adoption of these new life conditions we have not to deal therefore with survival or extermination, but only with amelioration. It is not every species of "White" that can become

adapted to these conditions, because every species does not give rise to the necessary colour variations; those that do, become in this way modified, because they are thus better protected than before. And so it is throughout; wherever we find protected insects enjoying immunity from foes we see also mimickers, sometimes only single, sometimes several, and generally from very diverse groups of insects, according to the general resemblance which existed before the commencement of the process of adaptation, and to the variations made possible by the physical nature of the species concerned.

In the first essay of the second part of this work it was shown that in certain Lepidopterous larvæ a process of adaptation is at the present time still in progress, this depending upon the fact that while the young caterpillar is very well protected by the leaf-green colour of its body, this colour becomes insufficient to conceal the insect as soon as it exceeds the leaf in size. All such caterpillars—and there is a whole series of species—as they increase in size acquire the habit of concealing themselves on the earth by day, and of feeding only at night. New conditions of life are thus imposed, and these are even compulsory, *i. e.* they could not be abandoned without risking the existence of the species. Now in accordance with these new conditions, some individuals in these species have lost the green colour-

ing of the young stages, and have acquired the brown coloration of the dark surroundings of the insects which conceal themselves by day. In one species this change has now occurred in almost all individuals, in others in only a larger or smaller proportion of them. Now supposing that among these species there occurred one, the physical nature of which did not admit of the production of brown shades of colour, would the species for this reason succumb? Is it not conceivable that the want of colour adaptation might be compensated for by better concealment, *i. e.* by burrowing into the earth, or by a greater fertility of the species, or by the development of warning signals—supposing the species to be unpalatable—or finally, by the acquisition of a terrifying marking? In other words, could not the caterpillar itself modify the new condition of life—that of being concealed by day—in accordance with variations made possible by its physical nature?

As a matter of fact in one of these species the green colour remains unchanged in spite of the altered mode of life, and this species, wherever it occurs, notwithstanding the persecution of entomologists, is always common (*Deilephila Hippophaës*); it conceals itself better and deeper however than those other species which, like *Sphinx Convolvuli*, are difficult to detect on account of their brown colour. In another species the striking yellowish green colouring is likewise retained in



the majority of individuals, but this species buries itself by day in the loose soil (*Acherontia Atropos*).

To this it may be objected that there are also compulsory changes in the conditions of life from which the species cannot withdraw itself, but in which adaptation must necessarily follow, or extermination would take place.

Such compulsory conditions of life do most assuredly occur, and there is indeed no doubt that many living forms have perished through not becoming transformed. I believe, however, that such conditions occur much more rarely than one is inclined to admit at first sight. As a rule the alternative of immediate change or of extermination is offered only by such changes in the conditions of life as occur very rapidly. The sudden appearance of a new and dominant enemy, such as man, has already caused the extinction of the Dodo (*Didus ineptus*), and of Steller's Sea Cow (*Rhytina Stelleri*), and of other vertebrate animals, and constantly leads to the extermination of many other species of different classes. When in America hundreds of thousands of acres of primeval forest are annually destroyed, the conditions of life of a numerous fauna and flora must be thereby suddenly changed, leaving no choice but extermination.

Such abrupt changes in the conditions of life occur, however, but seldom in nature unless caused by man, and must therefore have very

rarely happened in former epochs of the earth's history. Even climatic changes, which we might at first regard as of this character, and which produce a modification in one fixed direction, occur always so gradually that the species has time either to adapt itself to the conditions in this or that direction, according to the variations possible to its physical nature, or else to emigrate.

It thus appears to me erroneous to suppose that variability must be "merely undetermined" in order to complete its part in Darwin's theory of selection, and its "illimitedness" seems to me also as little necessary for this purpose. Von Hartmann imagines that it is only unlimited variability that furnishes a guarantee that any type, to whatever extent diverging from its point of departure, will be reached by the Darwinian method of gradual transmutation by means of selection and the struggle for existence.

But who has ever asserted that *any* type can be reached from any point? Or if anybody has said such nonsense, who can prove that its admission is necessary for the theory of selection? Nowhere in systemy do we see any point of support for such an assumption. But when Von Hartmann imagines that the "unlimited" variability which he postulates for Darwin "is in itself unlimited, the limits of its divergence in a given direction being found, not in itself, but only in external obstacles," he conceives variability to be

something independent of, and in some way added to, the animal body, and not a mere expression for the fluctuations in the type of the organism. If, however, we conceive variability in this latter, the true scientific sense, it is in no way "quantitatively unlimited," nor are its limits even determined by *external* influences, but essentially by *internal* influences, *i. e.* by the underlying physical nature of the organism. Darwin has indeed already shown this in a most beautiful manner in his investigations upon the correlations of organs and systems of organs of the body. To make use of a metaphor, the forces acting within the body are in equilibrium; if one organ becomes changed this causes a disturbance in the forces, and the equilibrium must be restored by changes in other parts, and these again entail other modifications, and so forth. Herein lies the reason why the primary change cannot exceed a certain amount if the restoration of the equilibrium is not to be quite impossible. This is but a metaphor, and I do not wish to assert that we are at present in a position to formulate and demonstrate mathematically for any particular case, how much an organ can become changed in any one species before an interruption of the internal harmony of the body takes place. But such impossibility of demonstration does not appear to me to furnish a sufficient reason for regarding variability as the expression of a directive power—as an "innate

tendency to variation conformable to law."<sup>2</sup> On the contrary, it is to me easily conceivable that we only learn to analyse the processes of nature in detail very slowly, because of their necessary complexity. It thus appears to me quite useless when in this sense Wigand makes use of the objection, that "the gooseberry has not undergone any enlargement since 1852, although it is inconceivable why it should not attain the size of a pumpkin if variability was not internally limited." It may well be that this is for the present "inconceivable;" nevertheless, this does not justify us in setting up a hypothetical "force of variation" which will not admit of the gooseberry surpassing the pumpkin in size. We are bound to maintain that it is the action and reaction of known forces which sets a limit to the enlargement of this fruit.

In more simple instances the causes of such limitations to growth can be well perceived. Several decades have passed since Leuckart proved in how exact a relation the proportion of volume and surface stood to the degree of organi-

<sup>2</sup> [The above views on the nature of variability, which were also broadly expressed in the first essay "On the Seasonal Dimorphism of Butterflies" (pp. 114, 115), are fully confirmed by Herbert Spencer (*loc. cit.* chaps. ix. and x.), and more recently by A. R. Wallace in an article on "The Origin of Species and Genera" (*Nineteenth Century*, vol. vii., 1880, p. 93). See also some remarks by Oscar Schmidt in his "Doctrine of Descent and Darwinism," *Internat. Scien. Ser.* 3rd. ed. 1876, p. 173. R. M.]



zation of an animal. In animals of a spherical form the surface is quite sufficient for respiration, so long as they are of microscopic size. But such an organism cannot become enlarged at pleasure, because the ratio of the surface to the volume would become quite different. The surface increases as the square, whilst the volume increases as the cube, so that very soon the surface of the more rapidly increasing bodily mass can no longer suffice for respiration.<sup>3</sup> This sort of limitation is in no way equivalent to that purely external kind which, for instance, manifests itself in such a manner as to prevent the indefinite lengthening of the tail feathers of the Bird of Paradise. In this case feathers that were too long would hinder flight, and such individuals would accordingly be eliminated by natural selection. The cause is in the former case purely internal, depending upon the equilibrium of the forces governing the organism.

Von Hartmann is entirely in the right when he asserts that variability is neither qualitatively nor quantitatively unlimited. In both senses it is limited (in direction as well as in amount) by the physico-chemical forces acting in some contrary way in each specific organism—by the physical

<sup>3</sup> [This law has been beautifully applied by Herbert Spencer in order to explain why, with an unlimited supply of food, an organism does not indefinitely increase in size. "Principles of Biology," vol. i. p. 121—126. R. M.]

nature of each living form. He errs, however, both in making absolute illimitability a necessary postulate of the theory of selection, as also in inferring the existence of a directive principle from that limitation of variability which is certainly present. "Tendencies to variation" do however exist, not in the sense of a directive power, but as expressions of the different physical constitutions of species, which necessarily cause unequal reactions to the same external actions, as will be more clearly proved below.<sup>4</sup>

This is, of course, a modification of Darwin's original assumption of an unbounded variability not limited in direction; but Darwin himself has later coincided in the view that the quality of the variations is essentially determined by the nature of the organism.<sup>5</sup>

<sup>4</sup> [Eng. ed. This idea, formerly expressed by me, occurs also in Lange ("Geschichte des Materialismus," ii. 265), and is there exemplified in a very beautiful manner by illustrations from modern chemistry. Lange compares what I have termed above the "physical constitution" of the organism to the chemical constitution of one of those organic acids which by substitution of single elements may become transformed into more complicated acids, but which, as it were, always undergo "further development" in only one determined and narrowly restricted course. Here, as with the organism, the number of possible variations is very great, but is nevertheless limited, since "what can or cannot arise is determined beforehand by certain hypothetical properties of the molecule."]

<sup>5</sup> "Origin of Species." 4th German ed., p. 19; 5th English ed., p. 6.

I now turn to the consideration of the second factor of the theory of selection—heredity. This also, according to Von Hartmann is not a mechanical principle. Darwin himself has now become convinced how great is the probability against the hereditary retention of modifications which, whether feebly or strongly pronounced, appear *only in single individuals, i. e.* of those so-called “fortuitous” variations which are not the expression of a directive developmental principle. “But as among the numberless possible directions of an indefinite variability, useful modifications can only occur in single cases, Darwin has by this supplementary admission himself retracted an inadmissible assumption of his theory of selection,” and so forth. A “regular, designed tendency to variation, acting from within and contemporaneously affecting a large number of individuals,” must therefore be assumed “in order to insure the by itself improbable inheritance.”

But even from the unbounded variability laid down by the author, it by no means follows that useful variations can only occur in single individuals. In the whole category of *quantitative* variations the reverse is always the case. Is it the lengthening of some part that is concerned; so would a large number of individuals always possess the useful variation, since we are not dealing with an *absolute* enlargement, but only

with the fact that the part concerned is longer than in other individuals.<sup>6</sup>

But if *qualitative* variations come into consideration, it may be asked whether Darwin's "supplementary admission" does not go too far. Such calculations as those quoted by Darwin from the article in the *North British Review* of March 1867 are extremely deceptive, since we have no means of measuring the amount of protection afforded by a useful variation, and we can therefore hardly compute with any certainty, in how great a percentage of individuals a change must contemporaneously occur in order to have a chance of becoming transferred to the following generation. If our blue rock-pigeon could exist in a polar climate, and if we had the power of introducing it gradually, but not suddenly, into these regions in a wild state, who can doubt that it would assume the white colour of all polar animals? Nevertheless, among wild rock-pigeons white varieties do not occur more frequently than among swallows, crows, or magpies. Or must the white colour of polar animals, the yellow colour of desert species, and the green

<sup>6</sup> [Mr. A. R. Wallace, in his article last referred to, quotes some most valuable measurements of mammals and birds, showing the amount of variation of the different parts. These observations were published by J. A. Allen, in a memoir "On the Mammals and Winter Birds of East Florida," &c. (Bulletin of the Museum of Comparative Zoology at Harvard College, Cambridge, Mass., vol. ii. No. 3.) R. M.]



colour of leaf-frequenting forms, be always referred to a "regular, designed, fixed tendency to variation acting from within," and causing a "large number of individuals" to vary in a similar manner?

There is, however, a grain of truth in the foregoing; variations which occur singly have but little chance of becoming predominant characters, and this is obviously what Darwin concedes. But this is by no means equivalent to the assumption that only those variations which from the first occur in numerous individuals have a chance of being perpetuated. Let us keep to the facts. We have not the slightest reason either for regarding the white colour of polar animals as the direct action of cold, or for considering that the green colour of foliage-living caterpillars depends upon direct action arising from the habit of resting upon the leaves;<sup>7</sup> both these characters are explicable only by natural selection, and there is nothing to favour the assumption (which Von Hartmann postulates as necessary for success) that many individuals varied into white at the same time. We know no single extra-polar species of a dark colour which frequently, *i. e.* in many individuals of every generation, varies into white, but we know many species which from time to time produce single white individuals. Now

<sup>7</sup> [See note 2, p. 310. R. M.]

when, on the other hand, we find that all polar animals to which the white coloration is advantageous, and indeed none but species of which the nearest allies vary only individually into white, possess this colour, must we not conclude from this alone that *single* variations can, under favourable conditions, become predominant characters?

It appears to me that in this question one weighty factor has been too little regarded, even by the supporters of the selection theory, viz., the slowness of most, and especially of climatic changes, which I have already insisted upon. If the transformation of a temperate into an arctic climate occurred so rapidly that the species exposed to it had the alternative either of becoming white in ten or twenty generations or of being unable to exist, then the hasty intervention of a directive power could alone save them from extermination by causing hundreds of thousands of individuals to become similarly coloured with all speed. But it is quite different if the change of climate takes place only in the course of several thousand generations; and this, according to the geological evidence, must have been the true state of the case.

Let us take a definite example—the well-known one of the hare. With us this animal remains brown in the winter and but seldom produces white varieties, whilst its ally the Alpine hare is

white during seven months of the year, the Norwegian hare during nine months, and the Greenland hare throughout the whole year. If our climate became transformed into an arctic one, after a given time there would arrive a period when the older coloration no longer possessed any advantage over the occasional and singly-appearing white variations; the winter days during which the ground was covered with snow would have become so numerous, that the protection afforded to the white animals would be equal to the protection enjoyed by the brown individuals on the equally numerous days free from snow. From this time forth the hares that were white in winter would not be subjected to a greater decimation by foxes, &c., than the brown individuals. This period must however be represented as consisting of one or more centuries, and it would be strange if from the individual white hares, which now had an equal chance of existing, some white families did not become established. But the state of affairs would gradually become reversed—the brown hares would experience greater decimation, and wherever there were white families these would possess an advantage in the struggle for existence. It does not follow that the dark individuals would be forthwith extirpated; on the contrary, the advantage in favour of the white would be but small throughout a long period of time, and these individuals would only gradually

increase to a higher percentage of the total population; nevertheless their numbers would constantly but very slowly augment. In the course of time this increase would become more rapid for two reasons—first, because even a very small advantage in favour of the increasing number of individuals would always leave a greater number of these victorious; and secondly, because on the whole as the climate became more arctic, the advantage of being white would continually become more decisive in determining which should live and which should succumb.

Thus I see no reason why individual variations which do not appear only once, but which frequently recur in the course of generations, should not acquire predominance under favourable conditions. All facts are in accord with this. Even the common hare shows us that it would be quite capable of becoming coloured in a similar manner. In the museum of Stuttgart there are three specimens of *Lepus timidus*, killed in Wurtemberg, which are completely white, and several others which are silver-grey or spotted with white. In eastern Russia the common hare possesses a light grey, almost white, winter coat, and Seidlitz<sup>8</sup> makes known the interesting observation that such light specimens occur *singly* in Livonia, where “the common hare has become naturalized since the commencement of the century.”

<sup>8</sup> “Die Darwin'sche Theorie,” Dorpat, 1875.



As I have already insisted upon above, from the point of view of the conditions of life there is no reason for assuming rapid transformations; the change of conditions is almost always extremely slow; and indeed in numerous instances no objective change occurs, but simply a subjective one, if we may thus designate those cases in which the alteration in the conditions of life depends upon a change in the animal form which is undergoing transformation, and not in that of the environment. This is the case in the above-mentioned instances of mimicry, where the whole change in the conditions of life arises from one species becoming similar to another. The process of natural selection has here as long a period of time as it requires to perfect its results. It is quite similar in all cases of special protective adaptations of form and colour. In all these it is always *improvement* that is concerned, and not the question "to be or not to be" with which we have to deal.

It is just cases of this last kind, however, which are best fitted for exposing the improbability and insufficiency of the assumption of a variational tendency as a distinct directive power. We have only to fix our attention upon some particular case of sympathetic colouring, or, still better, of mimicry. A "tendency to variation" implies that a large number of individuals produce varieties resembling the model to be imitated, and

this—at least according to Von Hartmann—must take place in each of the successive generations, so that by this means, combined with heredity, the useful variation becomes increased. But how comes it that this “tendency to variation” coincides with the existence of the model both in time and place? Can this be due to accident if the two have not a common cause? The upholders of a directive power will certainly not admit this; so that there remains only Leibnitz’s assumption of a pre-established harmony contained in the first organic germ, which, after innumerable transformations of the organic form and after millions of years, gave rise in the midst of the Amazonian region to an inedible Heliconide with certain yellow, black, and white markings on the wings, and at precisely the same time developed the tendency in a Pieride at the same spot on the globe to imitate this Heliconide as a model!

In addition to this assumption, which is certainly but little worthy of consideration, there is perhaps one other remaining, viz., that all or many Pierides and other species of butterflies possessed the same tendency to a Heliconoid variation and were always everywhere striving to develop this type, but succeeded only where they accidentally coincided in time and place with the model, the “tendency” being thus furthered by natural selection. But the facts negative this assumption, since such imitative variations have

never been observed to a perceptible extent in other species.<sup>9</sup>

All variations which are demonstrably useful can be similarly dealt with if their origin is explained by variational tendencies.

We perceive that the objection which Von Hartmann brings against heredity is only valid on the ground that this process affords no security for the preservation of variations which occur singly. That heredity itself is a mechanical process is not directly disputed; it is simply assumed that new characters can be transferred by inheritance only when they are produced by the metaphysical "developmental principle," and not when they arise "accidentally." This critic does not therefore direct his attack against heredity, but rather against the mechanical origin of variability.

Von Hartmann might have said here that a reference of the phenomenon of heredity to purely mechanical causes, *i. e.* a mechanical theory of

<sup>9</sup> [A certain number of instances of mimicry are known to occur between species both of which are apparently nauseous. A most able discussion of this difficult problem is given by Fritz Müller, in the case of the two butterflies *Ituna Ilione* and *Thyridia Megisto*, in a paper published in *Kosmos*, May, 1879 (p. 100). The author shows by mathematical reasoning that such resemblances between protected species can be accounted for by natural selection if we suppose that young birds and other insect persecutors have to learn by experience which species are distasteful and which can be safely devoured. See also Proc. Ent. Soc. 1879, pp. xx—xxix. R. M.]

heredity, is up to the present time wanting. That he has not done so proves on the one hand that he despised the dialectical art, but, on the other hand, that he himself has not overlooked the subserviency of the total phenomenon to law, and that he grants the possibility of finding a mechanical explanation therefor. If, in fact, the power of inheritance does not depend upon mechanical principles, I know not what organic processes we are entitled to regard as mechanical, since they are all dependent in essence upon heredity, with which process they are at one, and from which they cannot be thought of as isolated. Haeckel correctly designates reproduction as surplus individual growth, and accordingly refers the phenomena of heredity to those of growth. Conversely, growth may also be designated reproduction, since it depends upon a continuous process of multiplication of the cells composing the organism, from the germ-cell to the innumerable congeries of variously differentiated cells of the highly developed animal body. Who can fail to see that these two processes, the reproduction of the germ-cell and its offspring in the economy of the individual, and the reproduction of individuals and species in the economy of the organic world, show an exact and by no means simply superficial analogy?<sup>10</sup> But whoso grants this must also conceive both processes to depend upon the

<sup>10</sup> See Haeckel's "*Generelle Morphologie*," ii. 107.



same cause—he cannot assume for the one a causal power and for the other a directive principle. If nutrition and cell-multiplication are purely mechanical processes, so also is heredity. Although it has not yet been possible to demonstrate the mechanism of this phenomenon, it can nevertheless be seen broadly that by means of a minimum of living organic matter (*e. g.* the protoplasm of the sperm and germ-cell) certain motions are transferred, and these can be regarded as directions of development, as I have already briefly laid down in a former work.<sup>11</sup> The power of organisms to transmit their properties to their offspring appears to me to be only conceivable in such a manner “that the germ of the organism by its chemico-physical composition together with its molecular structure, has communicated to it a fixed direction of development—the same direction of development as that originally possessed by the parental organism . . . .” (*loc. cit.* p. 24). This is confessedly nothing more than a hint, and we do not learn therefrom the means by which developmental direction can be possibly transferred to another organism.

Recently Haeckel, that indefatigable pioneer to whom we are indebted for such a rich store of new ideas, has attempted to bridge over this gap in his essay on “The Perigenesis of the Plasti-

<sup>11</sup> “Über die Berechtigung der Darwin'schen Theorie,” Leipzig, 1868.

dule," Berlin, 1876. The basic idea, that heredity depends upon the transference of motion, and variability upon a change of this motion, completely corresponds with the conviction gained in the province of physical science, that "all laws must finally be merged in laws of motion" (Helmholtz<sup>12</sup>). I hold this view to be the more completely justifiable—although certainly not in the remotest degree as proved—because I formerly designated the acquired individual variations as the "diversion of the inherited direction of development." Haeckel's hypothesis in so far accomplishes more than Darwin's pangenesis, in which a transference of matter, and not of a species of motion peculiar to this matter, is assumed. But although the germ of a mechanical theory of heredity may be contained in Haeckel's hypothesis, this nevertheless appears to me to be somewhat remote from completely solving the problem. It brings well into prominence one portion of the process of inheritance; under the image of a molecular motion of the plastidule, which motion is modifiable by external influences, we can well understand the fact of a change gradually taking place in the course of generations. On the other hand, the assumption of consciousness in the plastidule,—however admissible philosophically—although only as a

<sup>12</sup> "Populäre wissenschaftl. Vorträge," vol. ii., Brunswick, 1871, p. 208.

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formula, scarcely furnishes any deeper knowledge. In the light of a theory, detailed instances which were formerly obscure should become comprehensible. I fail to see, however, how the various forms of atavism, *e. g.* the reversions which so commonly occur by crossing different races, become more comprehensible by assuming consciousness in the plastidule. If in both parents the plastidule long ago acquired different molecular motions, why, in its rencounters in the germ, does it recollect past times and reassume the older and long abandoned motion? That it does acquire the latter is indeed a fact if we once refer the directional development of the individual to molecular motion of the plastidule; the wherefore does not appear to me, however, to become clearer by assuming consciousness in the plastidule. A mechanical theory of heredity must rather be able to show that the plastidule movements of the male and female germ-cells, in their rencounter in the case of the crossing of widely divergent forms, become mutually modified in such a manner that the motion of the common ancestral form must occur as the resultant. To such demonstration there is however as yet a long step. Haeckel himself moreover points out that his hypothesis is by no means a "mechanical theory of heredity," but only an introduction to this theory, which he hopes "will be capable of being elevated to the rank of a genetic molecular

theory" (*loc. cit.* p. 17). But although we must also confess with the critic of the "Philosophy of the Unconscious," that "the facts of heredity have hitherto defied every scientific explanation,"<sup>13</sup> this furnishes us with no excuse for flying to a metaphysical explanation, "which is here certainly least able to satisfy the inability to understand the connection arising from natural laws."

It is not to be wondered at that Von Hartmann, on the ground of the "Unconscious" on which he takes his stand, speaks of the law of correlation as an unconscious acknowledgment of a "non-mechanical universal principle on the side of Darwinism." By "correlation" he understands something quite different to the idea which we attach to this expression. He supposes that "Darwinism sees itself compelled to acknowledge through empirical facts the uniform correlation of characters pertaining to the specific type; but it thereby contradicts its mechanical principles of explanation, all of which amount to the same thing as conceiving the type as a mosaic, chequered, superficial, and accidental aggregate of characters, which have been singly acquired, contemporaneously or successively, by selection or habit." I do not believe, however, that any such conception has ever been admitted either by

<sup>13</sup> "Das Unbewusste vom Standpunkte der Physiologie u. Descendenztheorie," Berlin, 1872, p. 89. The second edition appeared in 1877, in Von Hartmann's own name.



Darwin or any one else. The admission that not all, but only every deep-seated *physiological* detailed modification, is or may be bound up with a system of correlated changes, indeed implies that we on our side also acknowledge an internal harmony of parts—an equilibrium, as I have above expressed it.

But does this include the admission of a teleological principle, or exclude a mechanical explanation? Do we thereby acknowledge a "specific type" in the sense of an inseparably connected complex of characters, none of which can be taken away without all the others becoming modified? Does such a view agree generally with the empirical facts?

Neither of these views appears to me to represent the case.

I will first answer the second question. On all possible sides the earlier view of the absolute nature of species is contradicted; there is no boundary between species and varieties. But when Von Hartmann assumes that by the transformation of one species "into another" the "whole uniformly connected complex must become changed," he falls back into the old doctrine of the absolute nature of species, which is sharply contradicted by multitudes of facts. We not unfrequently observe varieties which differ from the parent-form by only a single character, whilst others show numerous differences,

and again others may be seen in which the differences predominate. This last deviation would then be designated by many systematists as a new species, but not so by others.

The "specific type" is thus indeed a kind of mosaic-work, but it is a structure to which all the single characters—the stones of the mosaic—belong and build up one harmonious whole, and not a meaningless confusion. Some of the stones or groups of stones can be taken away and replaced by others differently coloured without the structure being thereby necessarily distorted, *i. e.* destroyed as a structure; but the larger the stones which are exchanged the more necessary will corrections in the other parts of the structure become, in order that the harmony of the whole may be preserved.

Still more weighty than those insensible transitions which in various groups of animals so frequently connect species with species, appear to me, however, the facts made known in the second essay of the second part of this volume, which prove that the two forms in which one species appears can change entirely independently of one another. The caterpillar changes and becomes a new variety or even species (according to the form-value of the change), whilst the butterfly remains unaltered. How could this occur if some other law than that of physiological equilibrium linked together the parts or charac-

ters and permitted them to become severed? Must not the two stages become changed with and through one another, like the parts of one body, since they first together constitute the specific type? Is not the fact of this not happening a proof that the whole "uniformly connected complex" of the specific type is not bound and held together by a metaphysical principle, but simply by natural laws?

Now when Von Hartmann comprises the relations of different species to one another under the idea of correlation, such for instance as the relation of dependence in which orchidaceous flowers stand with respect to the insects which visit them, he completely abandons the scientific conception which should be associated with this expression, and compares together two heterogeneous things which have nothing in common excepting that they are both considered by him as a result of the "Unconscious." The consequence which is then deduced from this correlation of his own construction, viz., that an organic law of correlation is only another expression for a "law of organic development" in the sense of a metaphysical power, obviously cannot be admitted.

By correlation we understand nothing more than the dependence of one part of the organism upon the others and the mutual inter-relations of these parts, which depend entirely upon a "physiological relation of dependence," as Von Hartmann

himself has correctly designated it. Herein is evidently comprised the total morphology of the organism—the structure as a whole, the length, thickness and weight of the single parts, as well as the histological structure of the tissues, since upon all these depends the performance of the single parts. But when, under correlation, Von Hartmann comprises “also a morphological, systematic, inter-action of all the elements of the organism with reference both to the typical ground-plan of the organization as well as to the microscopic anatomical structure of the tissues,” he drags into the idea something foreign to it, not on the ground of facts, but actually in opposition to them, and supported only by a supposed “innate developmental principle” which “is not of a mechanical nature.”

The living organism has already been often compared with a crystal, and the comparison is, *mutatis mutandis*, justifiable. As in the growing crystal the single molecules cannot become joined together at pleasure, but only in a fixed manner, so are the parts of an organism governed in their respective distribution. In the crystal where nothing but homogeneous parts become grouped together their resulting combination is likewise homogeneous, and it is obvious that they offer but very little possibility of modification, so that the governing laws thus appear restricted and immutable. In the organism, whether re-



garded microscopically or macroscopically, various parts become combined, and these therefore offer numerous possibilities of modification, so that the governing laws are more complex, and appear less restricted and unchangeable. In neither instance do we know the final causes which always lead to a given state of equilibrium; in the case of a crystal it has not occurred to anybody to ascribe the harmonious disposition of the parts to a teleological power; why then should we assume such a force in the organism, and thus discontinue the attempt, which has already been commenced, to refer to its natural causes that harmony of parts which is here certainly present and equally conformable to law?

On these grounds the assertion that the theory of selection is not an attempt at a "mechanical" explanation of organic development appears to me to be incorrect. Variability and heredity, as well as correlation, admit of being conceived as purely mechanical, and must be thus regarded so long as no more cogent reasons can be adduced for believing that some force other than physico-chemical lies concealed therein.

But we certainly cannot remain at the purely empirical conception as laid down by Darwin in his admirable work on the "*Origin of Species*." If the theory of selection is to furnish a method of mechanical explanation, it is essential that its factors should be formulated in a precise mechani-

cal sense. But as soon as we attempt to do this it is seen that, in the first enthusiasm over the newly discovered principle of selection, the one factor of transformation contained in this principle itself has been unduly pushed into the background, to make way for the other more apparent and better known factors.

I have for many years insisted that the first, and perhaps most important, or in any case the most indispensable, factor in every transformation, is *the physical nature of the organism itself*.<sup>14</sup>

It would be an error to believe that it is entirely the external conditions which determine what changes shall appear in a given species; the nature of these changes depends essentially upon the physical constitution of the species itself, and a modification actually arising can obviously be only regarded as the resultant of this constitution and of the external influences acting thereon.

But if an essential or perhaps even a preponderating share in determining new characters is to be undoubtedly ascribed to the organism itself, for a mechanical representation of organic develop-

<sup>14</sup> "Über die Berechtigung," &c., Leipzig, 1868. In this work will be found briefly laid down the theoretical conception of variability here propounded somewhat more broadly. [In the last edition of the "Origin of Species" Darwin states, with respect to the direct action of the conditions of life as producing variability, that in every case there are two factors, "the nature of the organism and the nature of the conditions." 6th ed. p. 6. R. M.]

mental processes everything depends upon our being able to conceive this most important factor in a definite theoretical manner, and to comprise under one common point of view its apparently contradictory manifestations of constancy and variability.

Now every change of considerable extent is certainly considered by Darwin to be the direct or indirect consequence of external actions; but indirect action always presupposes a certain small variability (individual variability), without which larger modifications cannot be brought about. Empirically this small amount of variability is doubtless present, but the question arises, upon what does it depend? Can it be conceived as arising mechanically, or is it perhaps just at this point that the metaphysical principle steps in and offers those minute variations which make possible that course of development which, according to this view, is immutably pre-determined? It is certainly the absence of a theoretical definition of variability which always leaves open a door for smuggling in a teleological power. A mechanical explanation of variability must form the basis of this side of the theory of selection.

This explanation is not difficult to find. All dissimilarities of organisms must depend upon the individuals having been affected by dissimilar external influences during the course of the development of organic nature. If we ascribe to the

organism the power of giving rise by multiplication only to exact copies of itself, or, more correctly, the power of transmitting unaltered to its successors the motion of its own course of development, each "individual variation" must depend upon the power of the organism to react upon external influences, *i. e.* to respond by changes of form and of function, and consequently to modify its original (inherited) developmental direction.

It has sometimes been insisted upon, that the "individuals of the same species" or the offspring of one mother cannot be absolutely equal, because, from the commencement of their existence, they have been subjected to dissimilar actions of the environment. But this implies that by perfectly equal influences they would become equal, *i. e.* it supposes that variability is not inseparably bound up with the essence of the organism, but is only the consequence of developmental tendencies which are in themselves equal being unequally influenced. As a matter of fact the first germs of an individual certainly cannot be supposed to be perfectly equal, because the individual differences of the ancestors must be contained therein in different degrees according to their constitution, and we should have to go back to the primordial organism of the earth in order to find a perfectly homogeneous root, a *tabula rasa* from which the descendants would commence their development.



Whether such a homogeneous root ever existed is however doubtful ; it is much more probable that *numerous* organisms first arose spontaneously,<sup>15</sup> and these cannot be presumed to have been absolutely equal, since the conditions under which they came into life cannot have been perfectly identical. Let us, however, for the sake of simplicity assume a single primordial organism ; the first generation which took its rise from this by reproduction could only have possessed such individual differences as were produced by the action of dissimilar external influences. But the third generation, together with self-acquired, would also have shown *inherited*, dissimilarities, and in each succeeding generation the number of tendencies to individual difference imparted to the germ by heredity must have increased to a certain degree, so that it may be said that all germs,

<sup>15</sup> [Although hardly necessary to the evolutionist, it may perhaps be well to remind the general reader, that all experiments upon spontaneous generation, or abiogenesis, have hitherto yielded negative results ; no life is produced when the proper precautions are taken for excluding atmospheric germs. But although we have so far failed to reproduce in our laboratories the peculiar combination of conditions necessary to endow colloidal organic matter with the property of "vitality," the consistent evolutionist is bound to believe, from the analogy of the whole of the processes of nature, that at some period of the earth's history the necessary physical and chemical conditions obtained, and that some simple form or forms of life arose "spontaneously," *i. e.* by the operation of natural causes. R. M.]

from their first origination, bear in themselves a tendency to show individual peculiarities, and would develop these even if they should not be again affected by dissimilar influences. This is obviously the case, since the youngest egg-cells in the ovary of an animal are, as can be demonstrated, always exposed to unequal external conditions with respect to nutrition and pressure.<sup>16</sup> Hence, if it were possible that two germs were exactly equal with respect to the direction of development imparted to them by heredity, they would nevertheless furnish two incongruent individuals; and if, conversely, it were possible that two individuals could be exposed to absolutely the same external influences from the formation of the embryo, these also could not be identical, because the individual differences of the ancestors would entail small differences, even in asexual reproduction, in the direction of development transmitted to the egg. The differences between individuals of similar origin thus finally depend entirely upon the dissimilarity of external influences—on the one side upon those which divert the development of the progenitors, and on the other side upon those which divert the individual itself from its course, *i. e.* from the developmental direction transmitted hereditarily. Although I thus essentially agree with Darwin and Haeckel

<sup>16</sup> See Haeckel's "Generelle Morphologie," vol. ii. p. 203, and Seidlitz, "Die Darwin'sche Theorie," 1875, p. 92 *et. seq.*

in so far as these authors refer the "universal individual dissimilarity" to dissimilar external actions, I differ from Darwin in this, that I do not see an essential distinction between the direct and indirect production of individual differences, if by the latter is meant only the unequal influencing of the germ in the parental organism. Haeckel is certainly correct in referring the "primitive differences of the germs produced by the parents" to the inequalities of nutrition to which the single germs must inevitably have been exposed in the parent organism; but another dissimilarity of the germs must evidently be added—a dissimilarity which has nothing to do with unequal nutrition, but which depends upon unequal inheritance of the individual differences of the ancestors, a source of dissimilarity which must arise to a greater extent in sexual than in asexual reproduction. Just as in sexual propagation there occurs a blending of the characters (or more precisely, developmental directions) of two *contemporaneous individuals* in *one* germ, so in every mode of reproduction there meet together in the same germ the characters of a whole *succession of individuals* (the ancestral series), of which the most remote certainly make themselves but seldom felt in a marked degree.

The fact of individual variability can in this way be well understood; the living organism contains in itself no principle of variability—it is the *statical*

*element* in the developmental processes of the organic world, and would always reproduce exact copies of itself if the inequality of the external influences did not affect the developmental course of each new individual; these influences are therefore the *dynamical elements* of the process.

From this conception of variability two important empirically established facts can be theoretically deduced, viz. the limitability of variation with respect to quality, which has already been previously mentioned, and the origination of transformations by the direct action of external conditions of life.

If the differences in individuals of the same origin depend upon the action of unequal influences, variation itself is nothing else than the reaction of the organism to a definite external inciting cause, the quality of the variation being determined by the quality of the inciting cause and by that of the organism. In the cases of individual variation hitherto considered, the quality of the organism is equal but that of the inciting cause is unequal, and in this way there arise minute differences in organisms of an equal physical constitution—variations of a different quality.

The same result, viz., different qualities of variation, may also arise in a reverse manner by organisms of a different physical nature being affected by equal external influences. The response of the organism to the cause inciting



change would be different according to its nature, or, in other words, organisms of different natures react differently when affected by equal modifying influences. The physical nature of the organism plays the chief part with respect to the quality of the variations; each specific organism can thus give rise to extremely numerous, but not to all conceivable, variations; that is, only to such variations as are made possible by its physical composition. From this it follows further that the possibilities of variation in two species are more widely different, the wider they diverge in physical constitution (including bodily morphology)—that a cycle of variation is peculiar to every species. In this manner we are led to the knowledge that there must certainly exist a “fixed direction of variation,” but not in the sense of Askenasy and Von Hartmann, as the result of an unknown internal principle of development, but as the necessary, *i. e.* mechanical, consequence of the unequal physical nature of the species, which must respond even to the same inciting cause by unequal variations.

The facts, as far as we know them, agree very well with this conclusion. Allied species vary in a similar manner, whilst species which are more distantly related vary in a different manner, even when acted upon by the same external influences. Thus, in the first part of these “Studies” I have remarked that many butterflies under the influence

of a warm climate acquire an almost black coloration (*Polyommatus Phlæas*), whilst on the other hand others become lighter (*Papilio Podalirius*).

We can thus understand why always certain courses of development are followed, a fact which cannot be completely explained by the nature of the conditions of life which induce the variations. But as soon as we clearly perceive that the quality of the changes essentially depends upon the physical nature of the organism itself, we arrive at the conclusion that species of widely diverging constitutions must give rise to different variations, whilst those of allied constitutions would produce similar variations. But definite courses of development are thus traced out, and we perceive that from any point of the organic developmental series, it is impossible that any other point can be attained at pleasure. Variation in a definite direction thus by no means necessitates the acknowledgment of a metaphysical developmental principle, but can be well conceived as the mechanical result of the physical constitution of the organism.

The manner in which the dissimilar physical constitution of organisms must arise can also be easily shown, although the first commencement of the whole developmental series, *i. e.* the oldest living forms must be assumed to have been almost homogeneous in their physical constitution. The quality of the variation is, as said before,

not merely the product of the physical constitution, but the resultant of this and of the quality of the changing external conditions. Thus from the first "species" there proceeded, through the dissimilar influence of external conditions of life, several new "species," and as this took place the former physical nature of the organism at the same time became changed, necessitating also a new mode of reacting upon external influences, *i. e.* another direction of variation. The difference from the primary "species" must certainly be conceived as having been very minute, but it must have increased with each new transformation, and must have proceeded exactly parallel with the degree of physical change connected with each transformation. Thus, hand in hand with the modifications, the power of modification, or mode of reaction of the organism to changing influences, must have continually become re-modified, and we finally obtain an endless number of differently constituted living forms, of which the variational tendencies are different in exact proportion to their physical divergence, so that nearly allied forms respond similarly, and widely divergent forms very differently, to the same inciting causes.

Individual variation arises, as I have attempted to show, by each individual having been continually affected by different, and indeed by constantly changing, influences. Let us, how-

ever, imagine on the contrary, that a large group of individuals is affected by the same influences—in fact by such influences as the remaining individuals of the species are not exposed to: this group of individuals would then vary in a nearly similar manner, since both factors of variation, viz. the external influence and the physical constitution, are equal or nearly so. Such local variations would first become prominent when the same external influence had acted upon a series of generations, and the minima of variation produced in the individual by the once-exerted action of the cause inciting change had become augmented by heredity. Transformations of some importance (up to the form-value of species) can thus arise simply by the direct action of the environment, in the same way as that in which individual differences are produced—only the latter fluctuate from generation to generation, since the inciting influences continually change; whilst, in the former, the constant external cause inciting modification always reproduces the same variation, so that an accumulation of the latter can take place. Climatic varieties can be thus explained.

A more efficacious augmentation of the variations arising in the single individual is certainly brought about by the *indirect* action of the environment upon the organism. It is not here my intention to explain once more the processes of



natural selection; I mention this only in order to point out that in these cases transformation depends upon a *double action* of the environment, since the latter first induces small deviations in the organism by direct action, and then accumulates by selection the variations thus produced.

By regarding variability in this manner—by considering each variation as the reaction of the organism to an external action, as a diversion of the inherited developmental direction, it follows that without a change in the environment no advance in the development of organic forms can take place. If we imagine that from any period in the earth's history the conditions of life remain completely unchanged, the species present on the earth at this period would not, according to our view, undergo any further modification. Herein is clearly expressed the difference of this view from that other one according to which the inciting principle of modification is not in the environment, but lies in the organism itself in the form of a phyletic vital force.

I cannot here refrain from once more returning to the old (ontogenetic) vital force of the natural philosophers, since the parallel between this and its younger sister, the "phyletic vital force" which appears in so many disguises, is indeed striking. Were the inciting principle of the development of the individual actually an independent vital force acting within the organism,

the birth and growth of the individual would be able to take place without the continuous encroachment of the environment, such as occurs in nutrition and respiration. Now this is known to be impossible, so that those who support the existence of such a force, if any still exist, would be driven to the obscure idea of a co-operation between the designing power and the influences of the environment, just in the same manner as such a co-operation is at present postulated by the defenders of the phyletic vital force. I shall further on take the opportunity of pointing out that this last idea is quite untenable; with respect to the (ontogenetic) vital force any clearer proof cannot well be adduced, but it will be admitted that the confused notion of the co-operation and inter-action of teleological and causal powers is, from our point of view, opposed to those very simple and clear ideas which are in harmony with the views on phyletic development. As in racial development each change of the organic type is entirely dependent upon the action of the environment upon the organism, so in the development of the individual, the totality of the phenomena of the personal life must depend upon similar actions. Physiology, as is known, herein entirely supports our view, since this shows that without the continual alternating action of the environment and of the organism there can be no life, and that vital phenomena are nothing but the reactions of

the organism to the influences of the environment.

It will be immediately perceived how exactly the processes of phyletic and of ontogenetic development coincide, not merely in their external phenomena but in their nature, if we trace the consequences of the existing knowledge of the structure of the animal body. Although we may not entirely agree with Haeckel's doctrine of individuality in its details, its correctness must on the whole be conceded, since it cannot be disputed that the notion of individuality is a relative one, and that several categories of morphological individuals exist, which appear not only *singly* as *physiological individuals*, *i. e.* as independent living beings of lowest grade, but which can also *combine* to form beings of a higher order.

But if we admit this, we should see with Haeckel nothing but reproduction in the origination of a high organism from a single cell, the egg; this reproduction being at the same time combined with various differentiations of the offspring, *i. e.* with adaptations of the latter to various conditions of life. Not even in the fact that the tissues and organs of a single physiological individual stand in great dependence upon one another through physical causes,<sup>17</sup> is there any

<sup>17</sup> [In a recently published work by Dr. Wilhelm Roux this author has attempted to work out the idea of an analogy

striking difference between this view and the phyletic composition of the animal (and vegetable) kingdom out of physiological individuals (Haeckel's "*Bionten*"), since contemporaneous animals (individuals and species) are known to influence one another in the most active manner.

Now if we further consider that the same units (cells) which, by their reproduction and division of labour, at present compose the body of the highest organism, must at one time have constituted as independent beings the beginning of the whole of organic creation, and that consequently the same processes (division of cells) which now lead to the formation of a mammal, at that time led only to a long series of different independent beings, it will be admitted that both developmental series must depend upon the same inciting powers, and that with reference to the causes of the phenomena it is not possible that any great gap can exist between ontogeny and phylogeny, *i. e.* between the life-phenomena of the individual and those of the type. According to our view both depend upon that co-operation of the same material physical forces which admits of being between the struggle for existence and survival of the fittest in individuals and species, and the struggle for existence and survival of the parts in the individual organism. See "*Der Kampf der Theile im Organismus: ein Beitrag zur Vervollständigung der mechanischen Zweckmässigkeitslehre*," Leipzig, 1881. R. M.]



briefly summarized as the reaction of organized living matter to influences of the environment.

Our opponents either cannot boast of such harmony in their conception of nature, or else they must, together with the phyletic vital force, re-admit into their theory the old ontogenetic vital force. I know not indeed why they should not do so. Whoever inclines to the view that organic nature is governed not merely by causal, but at the same time by teleological, forces, may admit that the latter are as effective as inciting causes of individual, as they are of phyletic, development. According to my idea they are even bound to admit this, since it cannot be perceived why the adaptations of the ontogeny should not depend upon the same metaphysical principle assumed for each individual, as the adaptations of the phylogeny; the latter are indeed only brought about by the former. I believe therefore that the vital force (ontogenetic) of the ancients stands or falls with the modern (phyletic) vital force. We must admit both or neither, since they both rest on the same basis, and are supported or opposed by the same arguments. Whoever feels justified in setting up a metaphysical principle where complete proof that *known forces* are sufficient for the explanation of the phenomena has not yet been adduced, must do the same with respect to individual, as he does to phyletic, development, since this proof is in

both cases very far from being complete, and still contains large and numerous gaps.<sup>18</sup>

The theoretical conception of variation as the reaction of the organism to external influences has also not yet been experimentally shown to be correct. Our experiments are still too coarse as compared with the fine distinctions which separate one individual from another; and the difficulty of obtaining clear results is greatly increased by the circumstance that a portion of the individual deviations always depends upon heredity, so that it is frequently not only difficult, but absolutely impossible, to separate those which are inherited from those which are acquired. Still further are we removed from being able to refer variation to its final mechanical causes, *i. e.* from a mechanical theory of reproduction, which would bring within the range of mathematical calculation both the phenomena of stability (heredity) and of change (variability).

But although sufficient proofs of the correctness of the views here advocated cannot at present be adduced, these views are not contradicted by any known facts—they are, on the contrary, supported by many facts which they in turn make comprehensible (local forms, different

<sup>18</sup> [Eng. ed. Meanwhile it has been shown by Oscar Schmidt that Von Hartmann, under the name of "the Unconscious," re-invests the old vital force with some portion of its former power. "Die naturwissenschaftlichen Grundlagen der Philosophie des Unbewussten," Leipzig, 1877, p. 41.]

cycles of variation in heterogeneous species). These views are finally completely justified by their furnishing the only possible theoretical formulation of variability on which a mechanical conception of organic development can be based. That such a conception is not only admissible, but is unavoidable, at least to the naturalist, I have already attempted to prove.

## II.

## MECHANISM AND TELEOLOGY.

IN the third volume of his smaller works Karl Ernst von Baer submits the theory of selection to a most searching examination. Without actually calling in question its scientific admissibility, he believes that this theory is dependent upon its satisfying one condition, viz. that it should connect the teleological with the mechanical principle.

"The Darwinian hypothesis, as stated by its supporters, always ends in denying to the processes of nature any relation to a future, *i.e.* any relation of aim or design. Since such relations appear to me *quite evident*," &c. And further:—"If the scientific correctness of the Darwinian hypothesis is to be admitted, it must accommodate itself to this universal striving after a purpose. If it cannot do this we should have to deny its value."

These words appear almost equivalent to passing a sentence of doom upon the theory of



selection and the mechanical conception of nature, for how can one and the same process be effected simultaneously by necessity and by designing powers? The one excludes the other, and we must—so it appears—take our stand either on one side or the other.

Nevertheless we cannot set aside Von Baer's proposition without further examination simply because it is apparently incapable of being fulfilled, since it contains a truth which should not be overlooked, even by those who uphold the mechanical theory of nature. It is the same truth which is also made use of by the philosophical opponents of this theory, viz. that the universe as a whole cannot be conceived as having arisen from blind necessity—that the endless harmony revealed in every nook and corner by all the phenomena of organic and of inorganic nature cannot possibly be regarded as the work of chance, but rather as the result of a "vast designed process of development." It is also quite correct when, in reply to the supposed objection that the mechanical theory of nature is not concerned with chances but with necessities, Von Baer answers that the operations of a series of necessities which "are not connected together" can only be termed accidents in their opposing relations. He illustrates this by instancing a target. If I hit the latter by a well-aimed shot, nobody would explain this as the result of an

accident, but if "a horseman is riding along a gravelly road past this target, and one of the pebbles thrown up by the hoof of the galloping horse hits the mark, this would be termed an accident of extremely rare occurrence. My target was not the mark for the pebble, therefore the hit was purely accidental, although the projection of the stone in this precise direction with the velocity which it had acquired, was sufficiently explained by the kick given by the horse. But the hit was accidental because the kick of the galloping horse, although it necessarily projected the pebble, had no relation at all to my target. For the same reason we must regard the universe as an immense accident if the forces which move it are not designedly regulated—the more immense because it is not a single motion of projection that acts here, but a large number of heterogeneous powers, *i.e.* a large number of variously acting necessities which are, as a whole, devoid of purpose, but which nevertheless accomplish this purpose, not only at any single moment, but constantly. A truly admirable series of desirable accidents!"<sup>1</sup>

The same idea is expressed, although in a very different manner, by Von Hartmann, in the concluding chapter of his work already quoted. He thinks that "design is a necessary and certain consequence of the mechanical laws of nature."

<sup>1</sup> *Loc. cit* p. 175.

"Were the mechanism of natural laws not teleological there would be no mechanically regulated laws, but a weak chaos of obstinate and capricious powers. Not until the causality of the laws of inorganic nature had superseded the expression "dead" nature, and had shown itself as the main-spring of life and of a conformability to design visible on all sides, did it deserve the name of mechanical lawfulness; just as a complication of wheels and machinery made by man, which move in some definite manner with respect to one another, only acquires the name of a mechanism or of a machine when the immanent teleology of the combination and of the various movements of the parts is revealed."<sup>2</sup>

Against the correctness of the idea underlying these statements scarcely anything can in my opinion be said. The harmony of the universe and of that portion of it which we designate organic nature, cannot be explained by chance, *i.e.* without a common ground for co-operating necessities; by the side of mere mechanism it is impossible not to acknowledge a teleological principle—the only question is, in what manner can we conceive this as acting without abandoning the purely mechanical conception of nature?

This is obviously effected if, with Von Baer and Von Hartmann, we permit the metaphysical principle to interrupt the course of the mechanism

<sup>2</sup> *Loc. cit.* p. 156.

of nature, and if we consider both the former and the latter to work together with equal power. Von Hartmann expressly makes such an admission under the name of an "internal principle of development," to which he attributes such an important share that one cannot understand why it should have any need for the employment of causal powers, and why it does not simply do everything itself. Von Baer expresses himself much less decisively, and even in many places insists upon the purely mechanical connection of organic natural phenomena; but that with him also the idea of interruption by a metaphysical principle is present, is principally shown by his assuming, at least partly, the *per saltum* development of species. This necessarily involves an actively internal power of development.

Although I have already brought forward many arguments against the existence of such a power, and although in refuting it every form of development by directive powers is at the same time overthrown, it nevertheless appears to me not to be superfluous in such a deeply important question to show that a *per saltum* development, and especially the so-called heterogeneous generation, is inconceivable, not only on the ground of the arguments formerly employed against the phyletic vital force in general, but quite independently of these.

In the first place it must be said that the



positive basis of this hypothesis is insecure. Cases of sudden transformation of the whole organism with subsequent inheritance are as yet quite unknown. It has been shown that the occasional transformation of the Axolotl must most probably be regarded in a different light. Another case, taken for heterogeneous generation, viz. the budding of twelve-rayed Medusæ in the gastric cavity of an eight-rayed species, has lately been shown by Franz Eilhard Schulze<sup>3</sup> to be a kind of parasitism or commensalism. The buds of the *Cuninæ* do not spring, as was supposed, from the *Geryonia*, but are developed from a *Cunina* egg. But even if we recall here the cases of alternation of generation and heterogenesis, this would not be of any value by way of proof; it would only be thus indicated how one might picture to oneself a sudden transformation. That in alternation of generation, or generally, in every mode of cyclical reproduction, we have not to deal with the abandonment of one type of organization and the transition to some other, is proved by the continual return to the type of departure—by the cyclical character of the entire transformation. That two quite heterogeneous types can belong to one cycle of development is, however, capable of a far better and more correct

<sup>3</sup> "Über die Cuninen-Knospenähren im Magen von Geryonien." Reprint from "Mittheil. des naturwiss. Vereines," Graz, 1875.

explanation than would be given by the supporters of *per saltum* development. If we trace cyclical reproduction to the adaptation of different developmental stages or generations to deviating conditions of life, we thus not only explain the exact and often striking agreement between form and mode of life—we not only bridge over the gap between metamorphosis and alternation of generation, but we can also understand how, within one and the same family of Hydrozoa, species can occur with or without alternation of generation, and further how other species can exist in which the alternation of generation (the production of free Medusæ) is limited to the one sex; we can understand in general how one continuous series of forms may lead from the simple sexual organ of the Polypes to the independent and free swimming sexual form of the Medusæ, and how hand in hand with this the simple reproduction becomes gradually cyclical. It is just these intermediate steps between the two kinds of reproduction that make quite untenable the idea that the heterogeneous forms in cyclical propagation arise through so-called “heterogeneous generation,” *i. e.* through sudden *per saltum* transformation. It is excusable if philosophers to whom these facts are strange, or who have to take the trouble of working them up, should adduce alternation of generation as an instance of “heterogeneous generation,” but by

naturalists this should be once and for ever abandoned.

All other facts which have hitherto been referred to "heterogeneous generation" are still less explicable as such, inasmuch as they always relate to changes in single parts of an organism, such as the sudden change of fruit or flower in cultivated plants. The notion of *per saltum* development, however, demands a total transformation—it comprises (as Von Hartmann quite correctly and logically admits) the idea of a *fixed specific type* which can only be re-modelled *as a whole*, and cannot become modified piecemeal. It must further be added, that the observed variations which have arisen abruptly in single parts are not as a rule inherited:<sup>4</sup> fruit-trees are only propagated by grafting, *i.e.* by perpetuating the individual, and not by ordinary reproduction by seeds. Now, if we nowhere see sudden variations of large amount perpetuated by heredity, whilst we everywhere observe small variations which can all be inherited, must it not be concluded that *per saltum* modification is not the means which Nature employs in transforming species, but that an accumulation of small variations takes place, these leading in time to large differences? Is it logical to reject the latter conclusion because our period of observation is too

<sup>4</sup> [See Darwin's "Origin of Species," 6th ed. pp. 33, 34, and 201—204. R. M.]

brief to enable us to directly follow long series of accumulations, whilst *per saltum* variation is admitted, although unsupported by a single observation? As long as there remains any prospect of tracing large deviations to the continually observed phenomenon of small variations, I believe we have no right to resort to the purely hypothetical explanation afforded by *per saltum* variations.

But the hypothesis of "heterogeneous generation" is not only without a basis of facts—it can also be directly shown to be untenable. Since the operation of an internal power of transformation does not explain adaptation to the conditions of life, the claims of natural selection to explain these transformations must be admitted; but the co-operation of a phyletic vital force and natural selection is inconceivable if we imagine the modifications to occur *per saltum*.

The supposed "heterogeneous generation" is always illustrated by the example of alternation of generation. The origination of a new animal form is thus conceived to take place in the same manner as we now see, in the cyclical reproduction of the Medusæ, free swimming, bell-shaped Medusoids, produced from fixed polypites, or *Cercariæ* from Trematode worms by internal budding; in brief, it is imagined that one animal form suddenly gives rise to another widely deviating form by purely internal causes. Now on



this theory it would be an unavoidable postulate, that by such a process of *per saltum* development there arises not merely a new type of some species, but at the same time individuals capable of living and of persisting under, and fitted to, given conditions of life. But every naturalist who has attempted to completely explain the relation between structure and mode of life knows that even the small differences which separate one species from another, always comprise a number of minute structural deviations which are related to well defined conditions of life—he knows that in every species of animal the whole structure is adapted in the most exact manner *in every detail* to special conditions of life. It is not an exaggeration when I say in every detail, since the so-called “purely morphological parts” could not be other than they are without causing changes in other parts which exercise a definite function. I will not indeed assert that in the most closely related species all the parts of the body must in some manner differ from one another, if only to a small extent; it seems to me not improbable, however, that an exact comparison would very frequently give this result. That animals which are so widely removed in their morphological relations as Medusæ and Polypes, or Trematoda and their “nurses,” are differently constructed in each of their parts can, however, be stated with certainty.

Now if this wide deviation in every part were in itself no obstacle to the assumption of a designing and re-modelling power, it would become so by the circumstance that all the parts of the organism must stand in the most precise relation to the external conditions of life, if the organism is to be capable of existing—all the parts must be exactly adapted to certain conditions of life. How can this be brought about by a transforming force acting spasmodically? Von Hartmann—who, in spite of his clear perception and widely extended scientific knowledge, cannot possibly possess a strong conviction of that harmony between structure and life-conditions prevailing throughout the whole system of the organism, and which personal research and contemplation are alone able to give—simply bridges over the difficulty by permitting natural selection to come to his aid as an “auxiliary principle” of the re-modelling power. It would not be supposed that naturalists would resort to the same device—nevertheless those who support the phyletic force and *per saltum* development generally invoke natural selection as the principle which governs adaptation. But when does this agency come into operation? When by germinal metamorphosis a new form has arisen, this, from the first moment of its existence, must be adapted to the new conditions of life or it must perish. No time is allowed for it to continue in an unadapted state throughout a

series of generations until adaptation is luckily reached through natural selection. Let us have either natural selection or a phyletic force—both together are inconceivable. If there exists a phyletic force, then it must itself bring about adaptation.

It might perhaps be here suggested that the same objection applies to that process of modification which is effected by small steps, but that it does so only when the change occurs suddenly. This, however, as I have already attempted to show, but very rarely takes place; in many cases (mimicry) the conditions even change in the first place through the change in form and therefore, as is evident, as gradually as the latter. It must be the same in all other cases where transformation of the existing form and not merely extinction of the species concerned takes place. The transmutation must always keep pace with the change in the conditions of life, since if the latter change more rapidly the species could not compete with rival species—it would become extinct.

The abrupt transformation of species implies sudden change in the conditions of life, since a Medusa does not live like a Polype, nor a Trematode like its "nurse." For this reason it is impossible that natural selection can be an aiding principle of "heterogeneous generation." If such abrupt transformation takes place it must produce

the new form instantly equipped for the struggle for existence, and adapted in all its organs and systems of organs to the special conditions of its new life. But would not this be "pure magic"? It is not thereby even taken into consideration that here—as in the cases of mimicry—time and place must agree. The requirements of a pre-established harmony ("*prästabilierte Harmonie*") further demand that an animal fitted for special conditions of life should only make its appearance at that precise period of the earth's history when these special conditions are all fulfilled, and so forth.

But he who has learnt to perceive the numerous and fine relations which, in every species of animal, bring the details of structure into harmony with function, and who keeps in view the impelling power of these conditions, cannot possibly hold to the idea of a *per saltum* development of animal forms. If development has taken place, it must have occurred gradually and by minute steps—in such a manner indeed that each modification had time to become equilibrated to the other parts, and in this way a succession of modifications gradually brought about the total transformation of the organism, and at the same time secured complete adaptation to new conditions of life.

Not only abrupt modification however, but every transformation is to be rejected when based

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upon the interference of a metaphysical principle of development. Those to whom the arguments already advanced against such a principle appear insufficient may once more be asked, how and where should this principle properly interfere? I am of opinion that one effect can have but one sufficient cause; if this suffices to produce it, no second cause is required. The hand of a watch necessarily turns once round in a circle in a given time as soon as the spring which sets the mechanism in movement is wound up; in an unwound watch a skilful finger can perhaps give the same movement to the hand, but it is impossible that the latter can receive both from the operator and from the spring at *the same time, the same motion* as that which it would receive through either of these two powers *alone*. In the same manner it appears to me that the variations which lead to transformation cannot be at the same time determined by physical and by metaphysical causes, but must depend upon either one or the other.

On no side will it be disputed that at least one portion of the processes of organic life depends upon the mechanical co-operation of physical forces. How is it conceivable that sudden pauses should occur in the course of these causal forces, and that a directive power should be substituted therefor, the latter subsequently making way again for the physical forces? To me this is as

inconceivable as the idea that lightning is the electric discharge of a thunder-cloud, of which the formation and electrical tension depends upon causal forces, and of which the time and place are purely determined by such forces, but that Jupiter has it nevertheless in his power to direct the lightning flash according to his will on to the head of the guilty.

Now although I deny the possibility or conceivability of the contemporaneous co-operation of teleological and of causal forces in producing any effect, and although I maintain that a purely mechanical conception of the processes of nature is alone justifiable, I nevertheless believe that there is no occasion for this reason to renounce the existence of, or to disown, a directive power; only we must not imagine this to interfere directly in the mechanism of the universe, but to be rather behind the latter as the final cause of this mechanism.

Von Baer himself points this out to us, although he does not follow up the complete consequences of his arguments. He especially insists in his book, which abounds in beautiful and grand ideas, that the notions of necessity (causality) and of purpose by no means necessarily exclude one another, but rather that they can be connected together in a certain manner. Thus, the watch-maker attains his end, the watch, by combining the elastic force of a spring with wheel-work, *i. e.*

by utilizing physical necessities; the farmer accomplishes his purpose, that of obtaining a crop of corn, by sowing the seed in suitable land, but the seed must germinate as an absolute necessity when exposed to the influences of warmth, soil, moisture, &c. Thus, in these instances a chain of necessities is undoubtedly connected with a teleological force, the human will; and it directly follows from such cases that wherever we see an aim or result attained through necessities, the directive force does not interrupt the course of the series of necessities which have already commenced, but is active before the first commencement of these necessities, since it combines and sets the latter in movement. From the moment when the mechanism of the watch is combined harmoniously and the spring wound up, it goes without the further interference of the watchmaker, just as the corn-seed when once placed in the earth develops into a plant without assistance from the farmer.

If we apply this argument to the development of the organic world, those who defend mechanical development will not be compelled to deny a teleological power, only they would have with Kant<sup>6</sup> to think of the latter in the only way in which it can be conceived, viz. *as a Final Cause*.

In the region of inorganic nature nobody any

<sup>6</sup> [Eng. ed. See Kant's "Allgemeine Naturgeschichte und Theorie des Himmels."]

longer doubts the purely mechanical connection of the phenomena. Sunshine and rain do not now appear to us to be whims of a deity, but divine natural laws. As the knowledge of the processes of nature advances, the point where the divine power designedly interrupts these processes must be removed further back; or, as the author of the criticism of the philosophy of the Unconscious<sup>6</sup> expresses it, all advance in the knowledge of natural processes depends "upon the continual elimination of the idea of the miraculous." We now believe that organic nature must be conceived as mechanical. But does it thereby follow that we must totally deny a final Universal Cause? Certainly not; it would be a great delusion if any one were to believe that he had arrived at a comprehension of the universe by tracing the phenomena of nature to mechanical principles. He would thereby forget that the assumption of eternal matter with its eternal laws by no means satisfies our intellectual need for causality. We require before everything an explanation of the fact that relationships everywhere exist between the parts of the universe—that atoms everywhere act upon one another.<sup>7</sup> He who can content himself with the assumption

<sup>6</sup> "Das Unbewusste vom Standpunkte der Physiologie und Descendenz-Theorie," Berlin, 1872, p. 16.

<sup>7</sup> [Eng. ed. See Lotze's "Mikrokosmos," 1st ed., vol. iii. pp. 477—483.]



of matter may do so, but he will not be able to show that the assumption of a Universal Cause underlying the laws of nature is erroneous.

It will not be said that there is no advantage in assuming such a Final Cause, because we cannot conceive it, and indeed cannot so much as demonstrate it with certainty. It certainly lies beyond our power of conception, in the obscure region of metaphysics, and all attempts to approach it have never led to anything but an image or a formula. Nevertheless there is an advance in knowledge in the assumption of this Cause which well admits of comparison with those advances which have been led to by certain results of the new physiology of the senses. We now know that the images which give us our sense of the external world are not "actual representations having any degree of resemblance,"<sup>s</sup> but are only signs for certain qualities of the outer world, which do not exist as such in the latter, but belong entirely to our consciousness. Thus we know for certain that the world is not as we perceive it—that we cannot perceive "things in their essence"—and that the reality will always remain transcendental to us. But who will deny that in this knowledge there is a considerable advance, in spite of its being for the most part of a negative character? But just as we must assume behind the phenomenal world of our

<sup>s</sup> See Helmholtz's "Populäre wissenschaftl. Vorträge," vol. ii., Brunswick, 1872.

senses an actual world of the true nature of which we receive only an incomplete knowledge (*i.e.* a knowledge corresponding only in reality with the relations of time and space), so behind the co-operating forces of nature which "aim at a purpose" must we admit a Cause, which is no less inconceivable in its nature, and of which we can only say one thing with certainty, viz., that it must be teleological. Just as the former first leads us to perceive the true value of our sensual impressions, so does the latter knowledge lead us to foresee the true significance of the mechanism of the universe.

It is true that in neither case do we learn more than that there is something present which we do not perceive, but in both instances this knowledge is of the greatest value. The consciousness that behind that mechanism of the universe which is alone comprehensible to us there still lies an incomprehensible teleological Universal Cause, necessitates quite a different conception of the universe—a conception absolutely opposed to that of the materialist. Most correctly and beautifully does Von Baer say that "a purpose cannot be otherwise conceived by us than as proceeding from a will and consciousness; in this would the 'aiming at a purpose,' which appears to us as reasonable as it is necessary, have its deepest root." If we conceive in this world a divine Universal Power exercising volition as the ultimate

basis of matter and of the natural laws resident therein, we thus reconcile the apparent contradiction between the mechanical conception and teleology. In the same way that Von Hartmann, somewhere speaks of the immanent teleology of a machine, we might speak of the immanent teleology of the universe, because the single forces of matter are so exactly adjusted that they must give rise to the projected world, just as the wheels and levers of a machine bring forth a required manufactured article. I admit that these are grossly anthropomorphic ideas. But as mortals can we have any other ideas? Is not the notion of purpose in itself an equally anthropomorphic one? and is there any certainty that the idea of causality is less so? Do we know that causality is unlimited, or that it is universally valid? In the absence of this knowledge, should it not be permissible to satisfy as far as we can the craving of the human mind for a spiritual First Cause of the universe, by speaking of it in terms conceivable to human understanding? We can take up such a final position and still be conscious that we thereby form no certain conception, and indeed come no nearer to the reality. The materialist still makes use of the notion of "eternity," and frequently handles it as though it were a perfectly known quantity. We nevertheless do not seriously believe that by the expression "eternal matter," any true idea resulting from human experience is gained.

X

If it is asked, however, how that which in ourselves and in the remainder of the animal world is *intellectual* and *perceptive*, which *thinks* and *wills*, is ascribable to a mechanical process of organic development—whether the development of the mind can be conceived as resulting from purely mechanical laws? I answer unhesitatingly in the affirmative with the pure materialist, although I do not agree with him as to the manner in which he derives these phenomena from matter, since thinking and extension are heterogeneous things, and one cannot be considered as a product of the other. But why should not the ancient notion of “conscious matter” given out by Maupertuis and Robinet, not be again entertained, as pointed out in recent times by Fechner?<sup>9</sup> Would there not thus be found a useful formula for explaining phenomena hitherto quite incomprehensible?

Von Hartmann in criticizing himself, designates the sensibility of atoms as an “almost inevitable hypothesis” (p. 62), “inevitable because if sensibility were not a general and original property of the constituent elements of matter, it would be absolutely incomprehensible how through its potentiality and integration that sensibility known to us as being possessed by the organism could

<sup>9</sup> See also Fr. Vischer’s “Studien über den Traum. Beilage zur Augsburger Allgem. Zeitung,” April 14th, 1876. Haeckel also includes this idea in his recent essay already quoted, “Die Perigenesis der Plastidule,” Berlin, 1876, p. 38 *et seq.*



have arisen." "It is impossible that from purely external elements devoid of all internality (*Innerlichkeit*) there should suddenly appear, by a certain mode of combination, an internality which becomes more and more richly developed. The more certainly science becomes convinced that in the sphere of externality (*Äusserlichkeit*) the higher (organic) phenomena are only results of combination, or are the aggregate phenomena of the elementary atomic forces, the more surely, when she once seriously concerns herself with this other question, will she not fail to be convinced that the sensibility possessed by higher stages of consciousness can be only combination-results, or the aggregate phenomena of the elementary sensations of atoms, although these atomic sensations as such always remain below the level of the higher combinations of consciousness." In confusing this double-sided nature of the objective phenomenon "lies the main error of all materialism and of all subjective idealism. Just as the attempt of the latter (subjective idealism) to construct the external phenomena of existence in space out of functions of internality and their combinations is impossible, so is the endeavour of the former (materialism) to build up internal sensation out of any combinations of force acting externally in space equally impossible."

I have no intention of going any deeper into these questions. I mention them only in order to

point out that even from this side there appears to me no obstacle in the way of a purely mechanical conception of the processes of the universe. The naturalist may be excused if he attempts to penetrate into the region of philosophy; it arises from the wish to be able to contribute a little towards the reconciliation of the latest knowledge of the naturalist with the religious wants of the human mind—towards the aim striven for by both sides, viz. a satisfactory and harmonious view of the universe, according with the state of knowledge of our time.

X I believe that I have shown that the theory of selection by no means leads—as is always assumed—to the denial of a teleological Universal Cause and to materialism, and I thereby hope that I have cleared the way for this doctrine, the importance of which it is scarcely possible to over-estimate. Many, and not the most ill-informed, do not get so far as to make an unbiassed examination into the facts, because they are at the outset alarmed by the to them inevitable consequence of the materialistic conception of the universe. Mechanism and teleology do not exclude one another, they are rather in mutual agreement. Without teleology there would be no mechanism, but only a confusion of crude forces; and without mechanism there would be no teleology, for how could the latter otherwise effect its purpose?<sup>10</sup>

Von Hartmann correctly says:—"The most

<sup>10</sup> See Von Hartmann, *loc. cit.* p. 158.

complete mechanism conceivable is likewise the most completely conceivable teleology." We may thus represent the phenomenal universe as such a completely conceivable mechanism. With this conception vanish all apprehensions that the new views would cause man to lose the best that he possesses—morality and purely human spiritual culture. He who, with Von Baer, considers the laws of nature as the "permanent expressions of the will of a creative principle," will clearly perceive that a further advance in the knowledge of these laws need not divert man from the path of increasing improvement, but must further him in this course—that the knowledge of truth, whatever may be its purport, cannot possibly be considered a backward step. Let us take our stand boldly on the ground of new knowledge, and accept the direct consequences thereof, and we shall not be obliged to give up either morality or the comforting conviction of being part of an harmonious world, as a necessary member capable of development and perfection.

Any other mode of interference by a directive teleological power in the processes of the universe than by the appointment of the forces producing them, is however, at least to the naturalist, inadmissible. We are still far removed from completely understanding the mechanism by means of which the organic world is evoked—we still find ourselves at the very beginning of knowledge.

We are, however, already convinced that both the organic and the inorganic worlds are dependent only upon mechanical forces, for to this conclusion we are led, not only by the results of investigators who have restricted themselves to limited provinces, but also by the most general considerations. But although the force of these arguments may not be acknowledged, and although one might maintain that the inductive proofs against the existence of a "phyletic vital force" have been directed only against points of detail, or have never been completely demonstrated, *i. e.* for all points, it must nevertheless be conceded, that for the naturalist the mechanical conception of Nature is the only one possible—that he is not at all justified in abandoning this view so long as the interference of teleological forces *in the course* of the processes of organic development has not been demonstrated to him. Thus, it will not be immaterial whether a conception of Nature which to many seems inevitable is consistent with the idea of universal design, or a final directive universal principle, since the value which we may attach to our own lives and aims, essentially depends thereon. The final and main result of this essay will thus be found in the attempted demonstration that the mechanical conception of Nature very well admits of being united with a teleological conception of the Universe.



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## ERRATA.

Page 81, line 8 from top, and throughout essay, for "*Daphnide*" read "*Daphniide*."

Page 95, line 3 from bottom, for "Daphnoidea" read "Daphniacea."

Page 166, line 7 from bottom (note), for "p. 438" read "p. 433."

Page 245, line 17 from bottom (note), for "Ställ" read "Stoll."

Page 263, after the word "insects" (bottom line of note), add, "but the whole marking is suggestive of distastefulness."

Page 296, line 3 from bottom, for "Stähelina—collector" read "Stähelin—a collector."

Page 305, line 5 from bottom (note), for "In 1869" read "In 1865."

Page 434, bottom line of note, for "Geometræ" read "Bombycidæ."

Page 494, line 2 from top, for "from which a larval form" read "from a larval form which."

Page 542, line 12 from top, for "*Dione Vanilla*" read "*Dione Vanilla*."

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